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Morphological Transformation and Cladogenesis at the Base of the Adaptive Radiation of Miocene Hypsodont Horses

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ABSTRACT

The genus *Merychippus* has traditionally comprised a horizontal grade of incipiently hypsodont, middle Miocene, North American horses. Phylogenetic relationships both among merychippines and with younger, fully hypsodont clades were poorly delineated at best, thus prohibiting detailed analysis of the radiation of grazing equids. A single, most parsimonious, cladogram of 12 representative merychippine-grade species based on 39 cranial, dental, and postcranial characters was produced using the computer program PAUP. The early Hemingfordian species "*Parahippus*" *leonensis* was used as an outgroup; its previously undescribed cranial characters include a very shallow, unpocketed, poorly defined dorsal preorbital fossa, no malar fossa, and a shallow nasal notch. In these and other cranial characters it closely resembles "*Merychippus*" *primus*. The resultant cladogram supports the following hypotheses: *Merychippus* as traditionally used is a paraphyletic assemblage, and in a strictly phylogenetic classification should be limited to the type species and the few others with which it forms a monophyletic group. *Merychippus* sensu stricto is a hipparionine, most closely related to *Nannippus* and *Cormohipparion*. The tribes Hipparionini and Equini together form a monophyletic group within the Equinae, and each includes species of merychippine-grade. "*Merychippus*" *primus* is the sister taxon of the Equini + Hipparionini, and "*M.*" *gunteri* is the sister taxon to these three taxa. The Equini consists of two monophyletic subtribes, the Protohippina and the Equina. Known stratigraphic ranges provide chronological constraints for the timing of the major cladogenetic events. The first occurrence of both the Hipparionini and the Equini is late Hemingfordian, ca. 17.5 to 17.0 Ma.

The status of *Merychippus insignis* is reconsidered in light of the analysis by Evander (1986). In contrast to that study, we conclude that: (1) the development of a protostyle on deciduous premolars displays high levels of individual variation in some quarry samples (e.g., Thomas Farm "*P.*" *leonensis*), and thus it is not a judicious character with which to make systematic decisions without corroboration from others. (2) Specimens referred to *M. insignis* by Quinn (1955) and Evander (1986) from the Point Blank Fauna of Texas represent *Protohippus vetus*. (3) The Lower Snake Creek samples referred to *M. insignis* by Skinner and Taylor (1967) probably do represent that species.

INTRODUCTION

The radiation of the Equidae into the cursorial grazing ungulate adaptive zone in the middle Miocene of North America is a well known and familar example to most students of paleontology and evolution. This resulted in the presence in North America of at least 11 late Miocene, hypsodont, monophyletic clades (usually recognized as the genera *Pseudhipparion, Neohipparion, Hipparion, Nannippus, Cormohipparion, Protohippus, Calippus, Pliohippus, Astrohippus, Onohippidium,* and "*Dinohippus*"). As they are relatively distinct in morphology, recognition and study of these taxa from the later part of the radiation (the late Barstovian, Clarendonian, and Hemphillian, or ca. 14.5 to 4.5 Ma) is relatively straightforward, and work is nearing completion of an alpha-level taxonomic survey of these horses (MacFadden, 1980, 1984a, 1984b, 1986; Webb and Hulbert, 1986; Hulbert, 1987, 1988a, 1988b, 1988c; MacFadden and Hulbert, work in progress). However, during the late Hemingfordian and much of the Barstovian, from about 18 to 14.5 Ma, equids of a less hypsodont, phenetically more homogeneous grade, *Merychippus* s.l., predominated. Although tentative suggestions of phylogenetic relationships between particular species of *Merychippus* s.l. and certain advanced genera date back to Matthew (in Osborn, 1918: 98), the predominant 20th century classifications of the Equidae usually retained these taxa in a single, horizontal genus, *Merychippus*. This is hardly surprising, as it was the then accepted practice for groups at the base of adaptive radiations to be assigned to horizontal, paraphyletic groups on the basis of shared primitive (symplesiomorphic) character states and overall phenetic similarity (e.g., the traditional composition of the Reptilia, Insectivora, Condylarthra, and Miacidae). The reasons behind the classic subfamilial and generic classifications embodying the "evolution of the horse" are identical (but on a smaller scale) to those described by Kemp

(1988b: 2) for the Synapsida: a relatively complete fossil record, a large morphological difference between end members spanned by numerous structural intermediaries, and easily observed transformation sequences for some characters.

For horses, this remained the case until the mid-1970s, until the widespread application of phylogenetic systematics, and the realization that characters other than those of the cheekteeth were equally important in assessing relationships. Since then several species previously included in *Merychippus,* or new species of merychippine grade, have been explicitly allied to late Miocene genera using a philosophy of phylogenetic, or vertical classification (Skinner and MacFadden, 1977; MacFadden, 1984a; Webb and Hulbert, 1986; Hulbert, 1987, 1988a, 1989). The latter study was one of the first to present a cladogram demonstrating the relationships of a broad suite of merychippine species with those of younger genera. The present study is in part a refinement of that analysis, and attempts to answer the following questions regarding the adaptive radiation of hypsodont horses:

1. What are the phylogenetic interrelationships among the oldest-known merychippines, and how are they related to more "advanced" equids?
2. What was the precise timing, pattern, and geographical distribution of cladogenetic events during the early phases of the evolution of hypsodont horses?
3. What minimum age can be placed on the nearest common ancestor of all advanced, hypsodont equids?
4. How does the fossil record compare with the cladogram, and are there any major gaps in the record?
5. What are the primitive character state polarities for generic clades within the Equinae relative to their closest sister groups? This latter question is particularly important for phylogenetic analysis of these clades, and was our primary impetus for undertaking this study.

As reviewed below, many previous studies have focused on the base of the radiation of the Equinae. The intent here is not to rehash the same material and characters; rather there are three principal reasons that particularly justify this study. (1) In addition to examining well-known, previously studied specimens, included are important discoveries that fill many of the morphological, chronological, and geographical gaps in the fossil record that hindered previous investigations. (2) New geochronological and biochronological precision now allows calibration of critical Neogene faunas to within 1 m.y. or less (Flynn et al., 1984; Tedford et al., 1988). And, (3) the advent of computer programs for phylogenetic analysis allows simultaneous analysis of many more characters and taxa than could be reasonably expected in previous studies.

The alpha-level systematics of merychippine equids are by no means completely understood, and is the subject of on-going research by a number of investigators, notably Evander (1985, 1986, work in progress). These efforts will undoubtedly contribute to the reconstruction of equid phylogeny, and quite possibly contradict some of the results presented here. Nevertheless, since Leidy's initial description of *Merychippus insignis* over 130 years ago, significant progress has been made in the study of merychippine horses (summarized below), and many specialists have repeatedly demonstrated the validity of a number of species. These taxa are the focus of this study, whose primary goal is to answer the fifth question posed above.

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contributed important specimens including equids to the UF collection. Specimen illustrations are by W. Zomlefer; drafting by P. Ibarra. Statistical analyses were performed with SAS programs on the University of Florida Faculty Support Center's mainframe computer. Support for this project was provided by NSF Grant BSR-8515003 to BJM.

Abbreviations and Terminology

Institutional

AMNH	Department of Vertebrate Paleontology, American Museum of Natural History, New York
ANSP	Academy of Natural Sciences, Philadelphia
F:AM	Frick Collection, housed with AMNH collection
LACM (CIT)	California Institute of Technology collection, now housed at the Natural History Museum of Los Angeles County
MCZ	Museum of Comparative Zoology, Harvard University, Cambridge
TAMU	Texas A&M University collection, now housed with TMM collection
TMM	Texas Memorial Museum, University of Texas, Austin
UCMP	Museum of Paleontology, University of California, Berkeley
UCR	University of California, Riverside
UF	Vertebrate Paleontology Collection, Florida Museum of Natural History, University of Florida, Gainesville
UF/FGS	Florida Geological Survey Collection, now housed with UF collection
USNM	National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Statistical

$\bar{x}$	sample mean
s	sample standard deviation
N	sample size
CV	sample coefficient of variation
OR	observed range of a sample

Morphological

R, L	right, left
I/i	upper/lower incisor (e.g., i3 is a lower third incisor)
P/p	upper/lower premolar (e.g., P4 is an upper fourth premolar)
M/m	upper/lower molar (e.g., m2 is a lower second molar)
DP/dp	upper/lower deciduous premolar (e.g., DP2 is a deciduous upper second premolar)
DPOF	dorsal preorbital fossa (= lacrimal or nasomaxillary fossa)
MC	metacarpal
MT	metatarsal

General

Ma	Mega-anna, millions of years before present on the radioisotopic timescale
m.y.	millions of years (duration)
l.f.	local fauna
s.s.	sensu stricto
s.l.	sensu lato

Dental Measurements [Those in uppercase refer to upper dentitions; lowercase to lowers (see Hulbert, 1988a)]

APL	maximum anteroposterior length, excluding the ectoloph and hypocone
BAPL	anteroposterior length at the base of the crown
TRW	transverse width from mesostyle to lingualmost part of the protocone
PRL	maximum length of the protocone, excluding spur and connection to protoselene
PRW	maximum width of the protocone perpendicular to PRL
MSCH	crown height measured from the occlusal surface to the base of the crown along the mesostyle
UTRL	upper toothrow length from the anteriormost projection of the P2 to the posteriormost part of the M3
ROC	radius of curvature of the mesostyle
apl	maximum anteroposterior length from the paralophid to the hypoconulid
bapl	anteroposterior length at the base of the crown
atw	transverse width from the protoconid to the metaconid
ptw	transverse width from the hypoconid to the metastylid
entl	anteroposterior length of the entoflexid
mml	length from the anteriormost point of the metaconid to the posteriormost point of the metastylid
mcch	crown height measured from the occlusal surface to the base of the crown along the metaconid

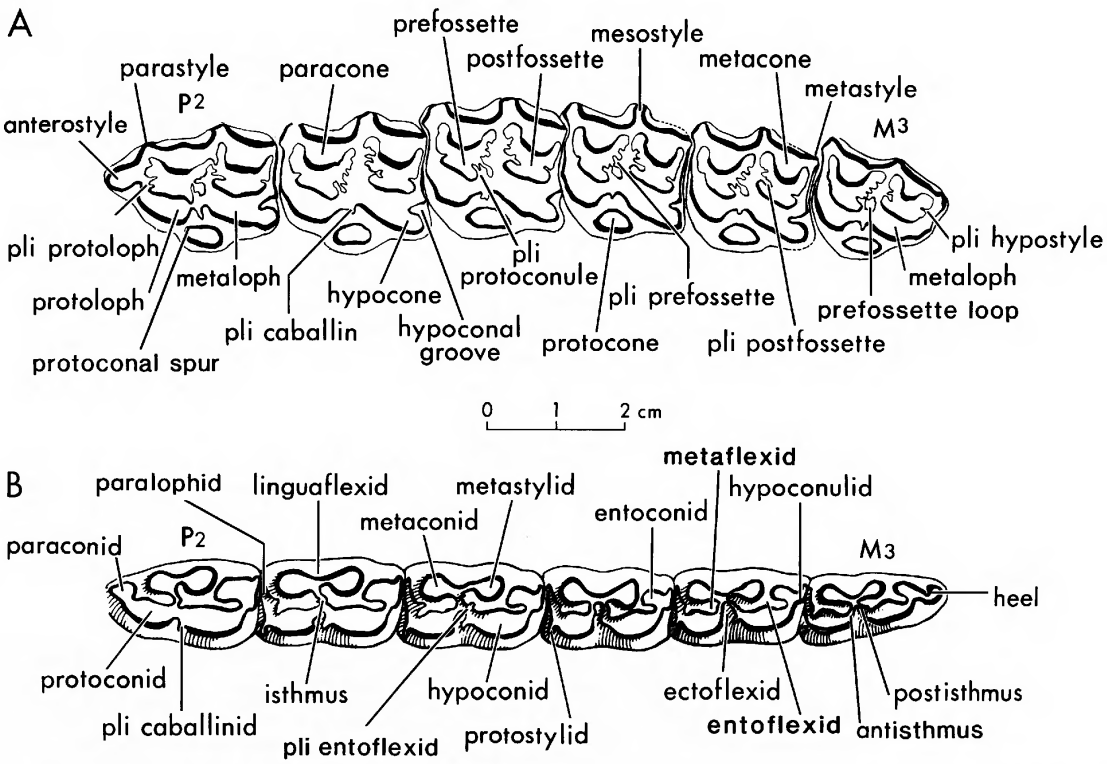


Fig. 1. Dental nomenclature of equid cheekteeth used in this study, slightly modified after MacFadden (1984a). **A.** Upper cheekteeth. **B.** Lower cheekteeth.

Dental terminology generally follows Stirton (1941) and MacFadden (1984a), and is illustrated in figure 1. General terms used to describe different ontogenetic phases of attritional cheektooth wear are very early (= earliest), early, moderate or middle, and late wear stages. Very early wear stage refers to the period between onset of wear and the time the entire occlusal surface is in wear and APL reaches its maximum observed value. At the end of this stage the tooth retains about 90 percent of its original crown height. Early wear stage refers to the period after the very early wear stage until the tooth is worn to about 75 percent of its original crown height. Moderate wear stage refers to the period following the early wear stage until the tooth is worn to about 25 percent of its original crown height. Teeth with less than 25 percent of their original crown height are referred to as heavily worn or as being in the late wear stage. These arbitrary classes are useful in describing the changes in enamel pattern associated with wear. The adjective "persistent" is used here to describe a character that appears on the occlusal surface at or near the onset of wear and remains visible to at least the end of the moderate wear stage. A very persistent character lasts well into the late wear stage. A nonpersistent character disappears either during the early wear stage or the first half of the moderate wear stage. If a sample is chosen randomly from a population, a very rare character state is defined as one that appears in less than 3 percent of the sample, a rare character state in about 3 to 10 percent of the sample, a common character state in about 50 to 75 percent of the sample, and a very common character state in about 75 to 95 percent of the sample.

The following terms are used to refer to various groups of horses:

Parahippine—a paraphyletic grade of species traditionally referred to the genus *Parahippus* s.l., also includes *Desmatippus* of some authors.

Merychippine—a paraphyletic grade of species traditionally referred to the genus *Merychippus* s.l.

Merychippus—a monophyletic group of merychippine species that includes the type species of the genus, *M. insignis*. This is a much more restricted grouping than the customary use of the genus.

"*Merychippus*"—a merychippine species that is not a member of *Merychippus* as defined above and

one that cannot be referred to any recognized monophyletic genus of equids without making that genus paraphyletic. Such species are here regarded as plesions of generic or higher rank.

Hipparionine—the tribe Hipparionini, a monophyletic clade containing *Hipparion, Cormohipparion, Nannippus, Neohipparion, Pseudhipparion,* Old World hipparions, and some merychippines including *Merychippus.* Use of *Cormohipparion* and *Hipparion* for North American taxa follows MacFadden (1984a); see Bernor and Hussain (1985; also Bernor, 1985) for an alternative interpretation.

Protohippine—the subtribe Protohippina, a monophyletic clade containing *Protohippus, Calippus,* and some merychippines.

Equine—the subtribe Equina, a monophyletic clade containing *Pliohippus, Astrohippus, "Dinohippus," Equus, Onohippidium, Hippidion,* and some merychippines.

PREVIOUS INVESTIGATIONS

Fossil horses, including the taxa discussed here, figured prominently in the studies of many 19th century mammalian paleontologists. In fact, the initial paleontological paper by the first preeminent vertebrate paleontologist in North America, Joseph Leidy (1847), was entitled: "On the fossil horse of America." During the latter part of the 19th century, paleontologists viewed horse phylogeny as an orthogenetic sequence of change beginning with "eohippus" (*Hyracotherium*) and culminating with *Equus.* For example, Marsh (1874: 294) wrote that: "The line of descent appears to have been direct, and remains now known supply every important intermediate form." This often-reproduced phylogenetic scheme (Marsh, 1879; fig. 2 here) did much to entrench orthogenesis in scientific writings during the latter part of the 19th and early 20th centuries.

In this section we: (1) review the historical development of evolutionary thought with regard to the essential features of the adaptive radiation of the Equinae during the middle Miocene; and (2) discuss various workers' ideas about the phylogenetic interrelationships of the relevant species of *Parahippus, Merychippus,* and *Protohippus.* It is not our intention here to review every species of these three genera, as this task would first require comprehensive revisions outside the purpose and scope of the present study.

The collections of Tertiary mammals made from the Nebraska and Dakota territories in the 1850s by the Hayden surveys included many specimens of fossil horses, and of relevance here, important early-named species of *Parahippus, Merychippus,* and *Protohippus.* The Bijou Hills of South Dakota produced the first two genera of equids to be named from North America, *Hippodon* and *Merychippus.* Leidy (1854) described *Hippodon speciosus* on a lower molar of uncertain stratigraphic provenience. Most later workers have regarded this specimen as an inadequate type, and have considered the taxon a nomen dubium. Later, Leidy (1857) proposed the genus *Merychippus,* and its type species *M. insignis,* on a maxillary fragment with deciduous teeth. In contrast to *Hippodon,* subsequent workers have generally accepted *Merychippus* as a valid genus, recognizing that the species *M. insignis* was poorly founded (e.g., Gidley, 1907: 879; for discussions see Skinner and Taylor, 1967; Evander, 1986).

Leidy (1858: 26) described *Parahippus* and *Protohippus* as subgenera of *Anchitherium* and *Equus,* respectively, on material from Nebraska. He later (e.g., Leidy, 1869) treated both as distinct genera rather than subgenera. Leidy (1858: 27) also described a second species of *Merychippus, M. mirabilis,* based on two partial maxillae from Nebraska (subsequently illustrated in Leidy, 1869: plate 17.8 and 17.10). Both specimens have well-developed malar fossae, a feature that Leidy (1869: 292) incorrectly assumed characterized the genus *Merychippus* as a whole.

Leidy's (1869) classification of horses is of some interest. He recognized two families in the order Solidungulata, the Anchitheridae (sic) and Equidae. The Anchitheridae (or Anchitheriinae of more modern authors) consisted of *Anchitherium, Hypohippus, Anchippus,* and *Parahippus.* These four genera were united on the following characters (Leidy, 1869: 303): short-crowned cheekteeth, lack of cement, and presence of roots in early wear stages. For Leidy, the Equidae (the Equinae of more modern authors, e.g., Simpson, 1945) consisted of *Equus, Protohippus, Hipparion,* and *Merychippus,* and differed from the former group by having high-crowned, cement-covered cheekteeth with ontogenetically de-

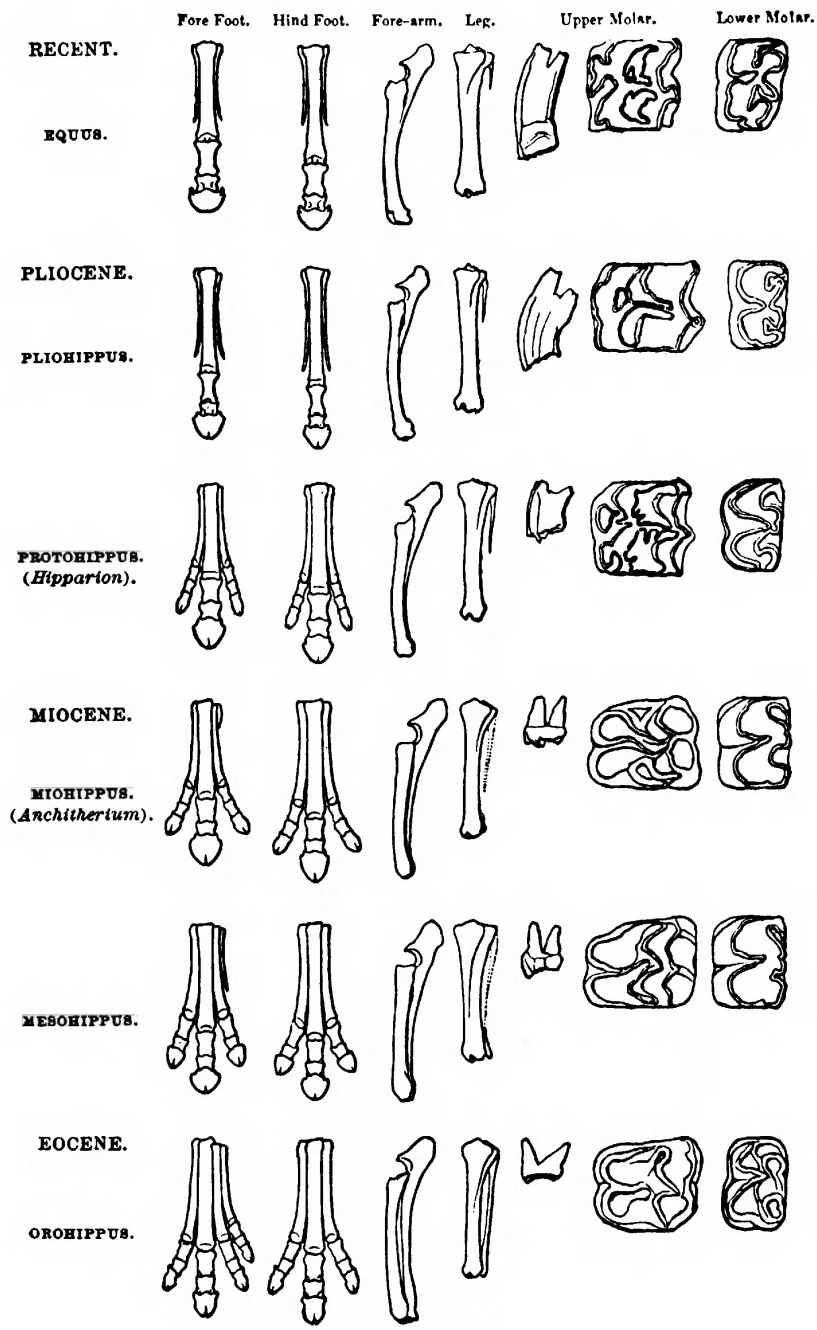


Fig. 2. Marsh's (1879) stratigraphically controlled succession of equid genera based on his collections from the western United States. This illustration did much to entrench orthogenetic thinking in the scientific literature.

layed root development (Leidy, 1869: 257). Leidy (1869: 313) explicitly realized that *Parahippus* and *Merychippus* formed the structural intermediates that linked the two families. For example, he noted that *Parahippus* shared with the Equidae the relative proportion of the protocone to the hypocone, a more enclosed postfossette through extension of the pli hypostyle, and more complete separation of the lingual median conid into two

distinct structures, the metaconid and metastylid. The primitive features of *Merychippus* that Leidy thought more closely resembled those of the anchitheres were largely confined to the low-crowned, poorly cemented deciduous premolars.

After these early descriptions of key equid taxa from the Great Plains, several new species from other areas were described that are of relevance to the current study. Marsh (1874) described two new species, *Protohippus avus* and *Anchippus brevidens* from the middle Miocene Mascall Fauna of Oregon. These two have subsequently been synonymized, and referred to *Parahippus* (see below). Sellards (1916) described a new species of *Parahippus, P. leonensis,* from the early Miocene of the Florida panhandle. Hay (1924) named a similar species, *Parahippus vellicans,* from the Texas Gulf Coastal Plain. Simpson (1930) described a new species of *Merychippus* from Florida, *M. gunteri,* which is often regarded as among the most primitive of the merychippines (e.g., Stirton, 1940). Because these species of *Parahippus* are advanced morphologically, and *M. gunteri* is very primitive relative to other members of their respective grades, they have figured prominently in subsequent discussions of the base of the adaptive radiation of equine horses and the transition from *Parahippus* to *Merychippus.*

Gidley (1907), in his excellent review of Miocene and Pliocene horses of North America, was among the first to realize equid phylogeny formed a complicated branching pattern rather than an orthogenetic sequence. Although rudimentary, his phylogenetic tree (reproduced here, fig. 3) depicted the Anchitheriinae as a side-branch and the Protohippinae (consisting of *Merychippus, Hipparion, Neohipparion, Protohippus,* and *Pliohippus*) were considered ancestral to *Equus* and *Hippidion.* Although he did not indicate it in his phylogenetic tree, Gidley (1907) recognized a major dichotomy within his Protohippinae separating hipparionines from *Protohippus* plus *Pliohippus,* and noted that the latter group had more affinities with *Hippidion.* However, he stated that the fossil record as known at that time was inadequate to determine the exact origins of the Protohippinae, and realized that most of the classic horse genera of Leidy were being used as structural grades rather than phylogenetic clades (Gidley, 1907: 869–870).

The classic monograph on Tertiary horses by Osborn (1918), although exhaustive, did not include a phylogenetic section and the detailed interrelationships at the base of the early Miocene adaptive radiation have to be extracted from his text (e.g., pp. 20 and 98). He described a series of five primitive subspecies of *Merychippus isonesus* from the Sheep Creek Beds of western Nebraska, *M. isonesus primus, M. i. secundus, M. i. tertius, M. i. quartus,* and *M. i. quintus.* These were later considered distinct species by most authors (e.g., Simpson, 1932; Stirton, 1940), but subsequent revisions of the fauna have suggested that only three are valid (Skinner et al., 1977). As will become important below, Osborn (1918) followed Gidley (1904, 1907) and considered *Merychippus* and *Protohippus* to be distinct genera, as did Matthew (1926).

Matthew's (1926) review of the fossil record of horses provided a foundation for the study of this group in a modern context. He viewed horse evolution as a series of ten stages, or morphological grades, and hence employed a horizontal classification scheme using modern systematic terminology. Of relevance here, his sixth and seventh stages were represented by, respectively, *Parahippus* and *Merychippus.* He noted that the boundary between these stages was fuzzy, with advanced members of the former difficult to distinguish from primitive members of the latter. Although two of his synthetic, phylogenetic figures (1 and 27) in that publication suggest that horses demonstrated orthogenetic evolution, Matthew was aware that there was a diversification of contemporaneous later Tertiary equids in North America. This is implied in his chart of chronologic ranges of equid genera (his fig. 25, p. 167), that depicts quasi-phylogenetic relationships. Matthew later expressed this concept more explicitly (in Matthew and Stirton, 1930: 356): ". . . it appears that the Lower Pliocene [late Miocene or Clarendonian of present usage] Equinae represent six nearly related groups of about equal value which have been rather artificially associated into three genera. All are derivable from different species of *Merychippus,* transitional stages being found in

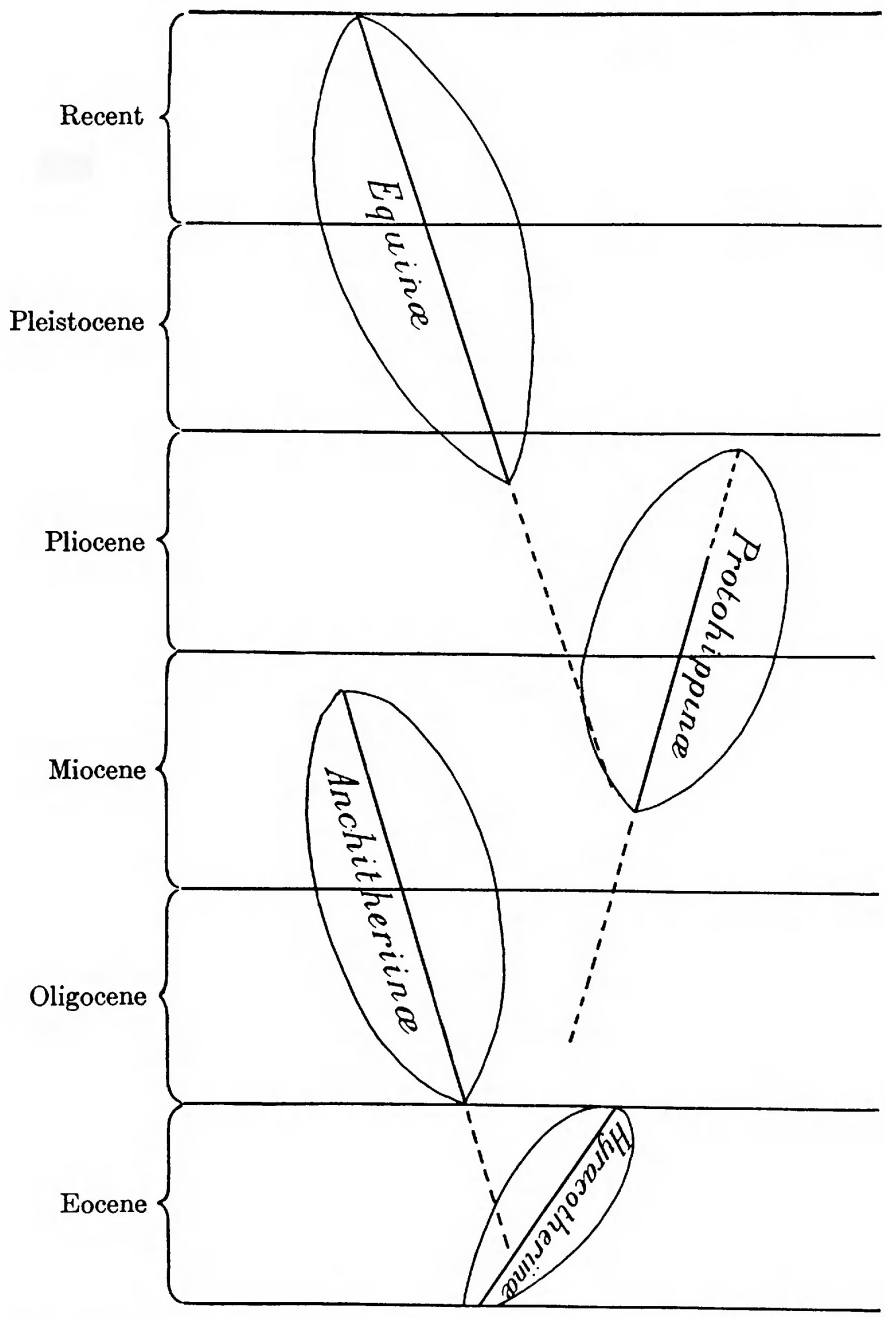


Fig. 3. Gidley's (1907) view of the phylogeny of the Equidae which was one of the first to recognize several major branching events, rather than a simple orthogenetic sequence.

the Upper Miocene [middle Miocene or Barstovian of present usage]."

Based on reanalysis of dental characters exhibited by previously described species from northern Nebraska, McGrew and Meade (1938) proposed that *Protohippus* be synonymized within *Merychippus,* the earlier-named genus. This decision was followed by Simpson (1945) and in a sense by Stirton (1940), in which he considered *Merychippus* to consist of two subgeneric clades, *M.* (*Merychippus*) and *M.* (*Protohippus*). Stirton's

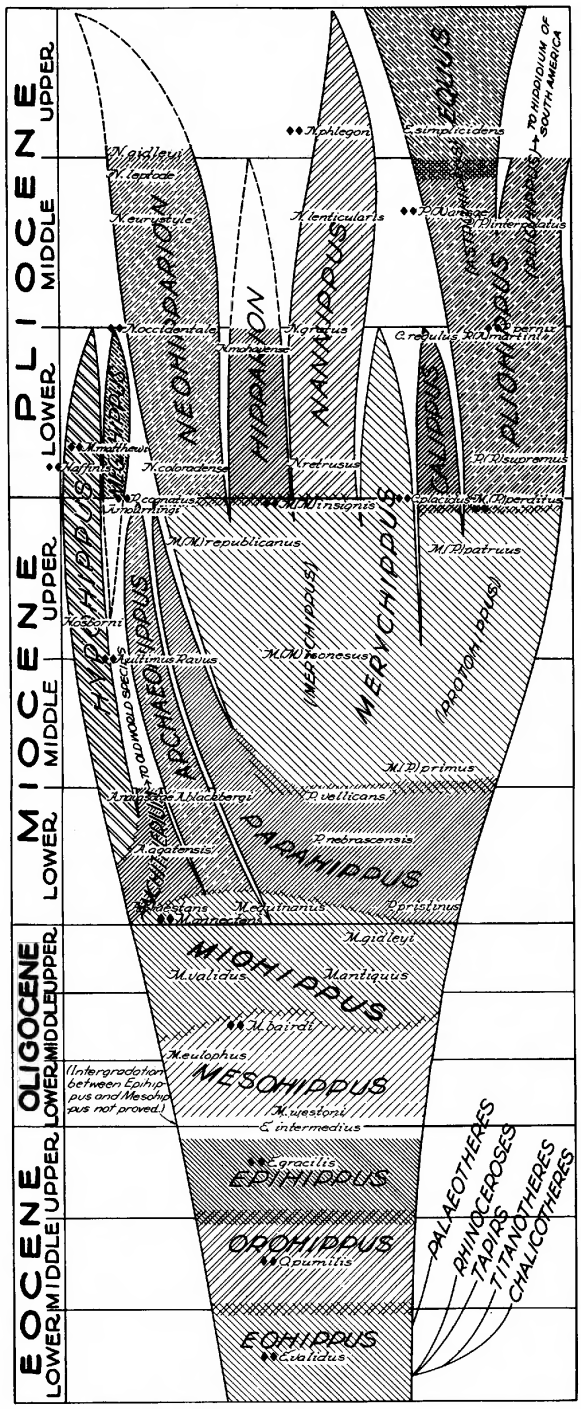


Fig. 4. Stirton's (1940) classic phylogeny of North American Equidae which details a complex pattern of branching during the Miocene. Almost all subsequently proposed phylogenies, with the important exception of Quinn's (1955, reproduced as fig. 5), are slight modifications of this one. Two important features of particular relevance to this

(1940) phylogeny of North American Equidae still stands as the primary reference on this group. This synthesis in a large part succeeded by reviewing a tremendous body of alpha-level taxonomic literature and producing a phylogenetic tree, the essential patterns of which have been frequently reproduced in subsequent publications (e.g., Simpson, 1951). Stirton, like Matthew, believed that *Parahippus* and *Merychippus* were best viewed as horizontal, polyphyletic grades, and (p. 177) stated that: "From the middle Miocene to the close of the epoch, different species of *Parahippus* seem to be intergrading with different species of *Merychippus.*" According to Stirton (1940: 180, also his phylogenetic chart reproduced here as fig. 4), *M.* (*Merychippus*) gave rise to the hipparionines, and *M.* (*Protohippus*) gave rise to *Calippus* and *Pliohippus.* Although this traditional concept of equine evolution has proven durable, it tends to obscure any notion of interrelationships among the advanced genera, and promotes arbitrary and artificial definitions for the genera *Parahippus* and *Merychippus.*

The important species *Parahippus leonensis* was first described from the Florida panhandle (Sellards, 1916), but it is better known from the rich early Hemingfordian Thomas Farm l.f. in northern peninsular Florida (Simpson, 1932; White, 1942; Hulbert, 1984). White (1942) believed that three species, *P. leonensis*; *Merychippus gunteri*; and a new, smaller, and dentally more primitive species, *Parahippus barbouri,* all occurred at Thomas Farm. In order to account for this diversity, he suggested that deposition at this site spanned a considerable amount of geological time, and that the three occurred in stratigraphic succession and formed an evolutionary continuum. Prior to the work of Pratt (1986, 1990), no stratigraphical data were collected with Thomas Farm specimens. Thus

←

study are (1) Stirton's representation of *Parahippus* and *Merychippus* as intergrading, horizontal grades, and (2) an abrupt and arbitrary transition from horizontal to vertical classification at what is here depicted as the Miocene-Pliocene boundary (at ca. 12 Ma, this is now considered to be middle Miocene).

White's hypothesis was necessarily speculative, and is not corroborated by recent stratigraphically controlled excavations (see also Bader, 1956). Also, detailed geological and paleoecological analyses (Pratt, 1986, 1989, 1990) suggest that Thomas Farm sediments represent a relatively short interval of geological time. White (1942) also synonymized *Parahippus vellicans* from the Texas Gulf Coastal Plain with *P. leonensis,* a conclusion endorsed by most subsequent investigators. Based on many additional specimens, Bader (1956) presented a detailed statistical study of the Thomas Farm horses and concluded that *P. barbouri* was a junior synonym of *P. leonensis.* He also demonstrated that the Thomas Farm specimens White referred to *M. gunteri* (1942) represented structurally advanced individuals within a variable *P. leonensis* population. Previously the evolutionary position of *P. leonensis* had been based primarily on the morphology of its cheek-teeth and postcranial elements (Sondaar, 1968). The cranial morphology of *P. leonensis* is described below for the first time, and it provides new insights into the equine radiation.

Quinn (1955) published an exhaustive description of certain fossil Equidae collected from the Hemingfordian through Clarendonian sequence of the Texas Gulf Coastal Plain. (Despite the inclusive title of his study, hipparionines were not studied in any detail by Quinn.) This study was a landmark in equid systematic methodology because it was the first to reflect a principally vertical classification of Miocene and later horses and to separate monophyletic groups within the merychippine complex (fig. 5). However, his taxonomy was too much of a radical change to gain acceptance, and some of his alpha-level taxonomic decisions later proved to be incorrect (see, e.g., critiques in Webb, 1969; Forstén, 1975; MacFadden, 1984a; Hulbert, 1988a). With the widespread acceptance of phylogenetic systematics and its use of vertical classification, Quinn's innovations have been reexamined within a cladistic context. As will be shown below, many of Quinn's new ideas regarding equid phylogeny are falsified by cladistic analysis (see also Hulbert, 1989), but he did attempt to provide a nomenclature that accurately reflected the evolutionary history of the group as he saw it. Several important aspects of Quinn's study are: (1) The description of a new early Barstovian species, *Protohippus vetus.* (2) The resurrection of the old, little-used Leidy (1854) genus *Hippodon* to include the Florida species usually referred to as *Parahippus leonensis* and *Merychippus gunteri,* and the extension of the distribution of the latter species into the Gulf Coastal region of Texas. (3) The consideration of *Protohippus* as a distinct genus (far off the "main-line" to *Equus*) that gave rise to species now allied within *Pliohippus* and the South American Pleistocene genus *Hippidion* (fig. 5). (4) The hypothesis that the late Barstovian Cold Spring species "*Eoequus wilsoni*" (actually *Protohippus perditus,* Hulbert, 1988a) was the direct ancestor of *Equus* s.l., and the two shared a closer common ancestor with the hipparionines than the protohippines. (5) Considering the Gulf Coastal Plain the center of origin of hypsodont horses.

Downs (1956), in his review of the Mascall Fauna of Oregon, analyzed the transition from *Parahippus* to *Merychippus* with a detailed comparison of all relevant species from North America. He reached the following important conclusions: (1) *Protohippus avus* and *Anchippus brevidens,* both named by Marsh (1874), were synonymous, and transferred to *Parahippus* as *P. avus.* (2) The Mascall species *Merychippus relictus* was very similar to *M. primus* from Nebraska. (3) As previously determined by Schlaikjer (1937), *P. leonensis* was the most advanced member of its genus and most probably the common ancestor of *Merychippus* s.l. In contrast to some previous authors, who mostly viewed their local taxa in isolation, Downs clearly recognized the close resemblance of advanced species of *Parahippus* and primitive species of *Merychippus* from Oregon with contemporaneous species elsewhere in North America.

Skinner and Taylor (1967) studied the geology and paleontology of the Bijou Hills of South Dakota, the type locality of *Hippodon speciosus* and *Merychippus insignis.* From a detailed study of these horse species they concluded that the former species is so poorly characterized (they regarded it as a nomen dubium) that the genus *Hippodon* should not be resurrected (contra Quinn, 1955). Al-

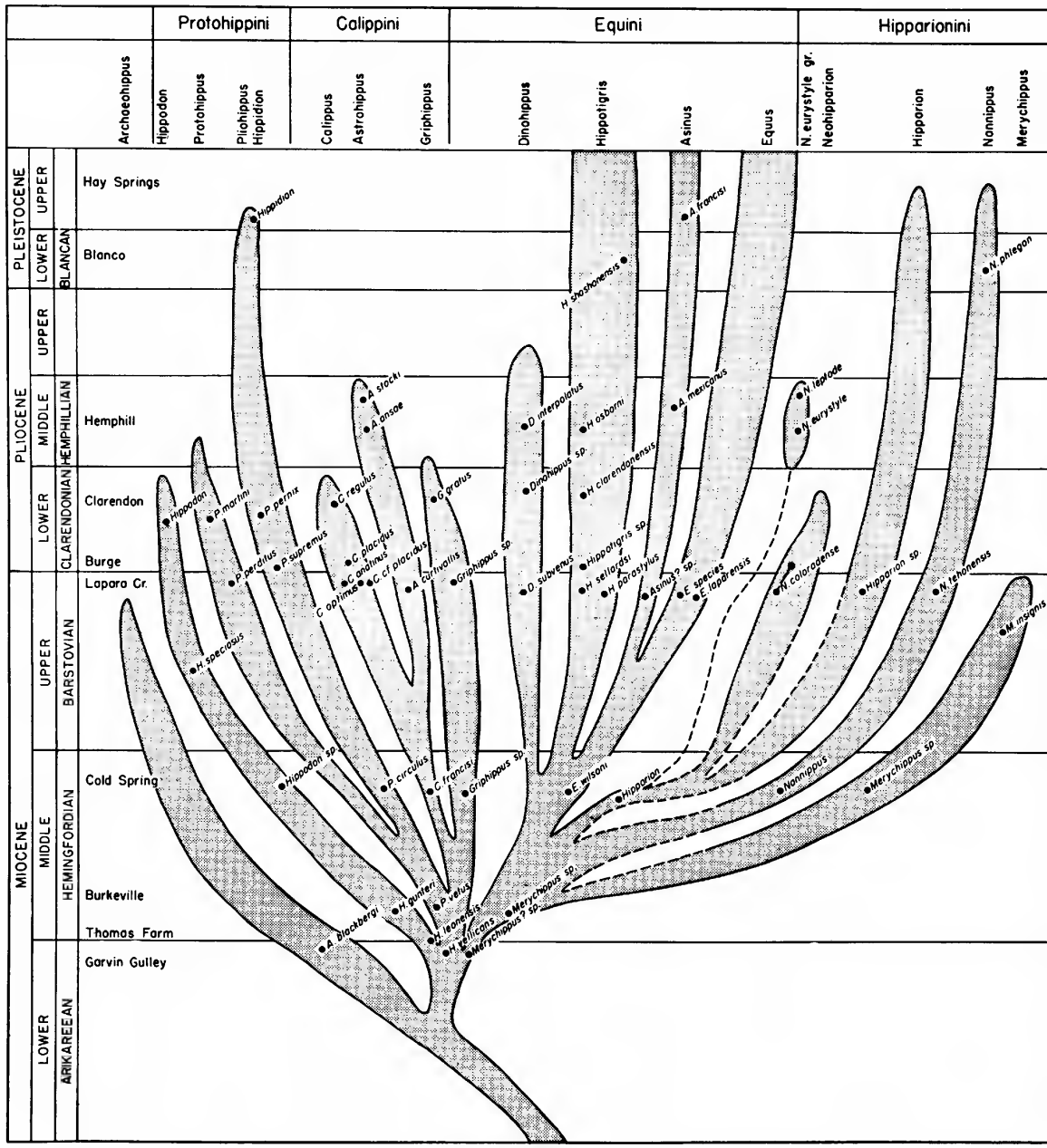


Fig. 5. Quinn (1955) presented this alternative phylogeny of the Equinae. In contrast to that of Stirton (1940; see fig. 4) or Simpson (1951), Quinn divided merychippine-grade equids into vertical, evolutionary clades and united them with their late Miocene sister groups. Despite his progressive approach, many of the phylogenetic relationships proposed by Quinn have not been corroborated by modern cladistic analysis (Hulbert, 1988a, 1989).

though the holotype of *M. insignis* is based on a fragmentary maxilla with DP2-DP3, they described for the first time the permanent upper dentition of topotypic material, and their comparisons allowed referral of a large, well-preserved sample from Echo Quarry in western Nebraska to this species (although see discussion in Evander, 1986, and below).

Forstén (1975) restudied the material from the Texas Gulf Coastal Plain previously an-

alyzed by Quinn (1955), and also made extensive comparisons with similar-aged material from Florida (e.g., Thomas Farm, Midway). She concurred with White (1942) that *Parahippus leonensis* is the senior synonym of *P. vellicans* (contra Quinn, 1955). In contrast to White (1942), she believed that *Merychippus gunteri* was not represented at Thomas Farm, a conclusion also followed by other workers studying that assemblage (Bader, 1956; Hulbert, 1984). She agreed with Quinn (1955) that *M. gunteri* was present in the Burkeville Fauna. Forstén (1975: 26) also reaffirmed the primitive phylogenetic position of *M. gunteri* among merychippines when she stated that this species: ". . . belongs in a group of relatively brachyodont merychippines, which could be related to each other. These are, besides *M. gunteri, M. primus, M. tehachapiensis, M. carrizoensis,* and *M. brevidontus.*" She did not, however, suggest any specific phylogenetic relationships between these taxa or with more advanced merychippines or equines.

In a predominantly stratigraphic report, Galusha (1975) made some very insightful observations on the equids from the late Hemingfordian Box Butte Formation of north-central Nebraska. From the base of the Red Valley Member, a partial skeleton was collected that Skinner (in Galusha, 1975: 58) identified as an advanced parahippine (i.e., incipiently hypsodont with cement) close to *P. vellicans.* Our recent study of this specimen suggests referral instead to a primitive "*Merychippus,*" however, specific identification is impossible because of the late wear stage of the dentition. More importantly, Galusha also noted (p. 58): "Several examples of *Merychippus* sp. near *M. primus* have been identified from the Red Valley Member in the paleochannel system north of the Niobrara River. . . . These do not exactly duplicate *M. primus* but belong in a melange of specimens in the American Museum Frick collections that display an astounding array of characters that suggest that this particular group of horses was changing rapidly, especially during the interval in which the Sheep Creek Formation was deposited." In addition to *M.* sp. near *primus,* Galusha recognized two other lithosympatric merychippines in the Red Valley Member, one near *M. isonesus* and another he could not match with any described species. We have reexamined these specimens, and agree with Galusha's general conclusion that three merychippines are present in the fauna (see descriptions below). These observations are important because in pre-Box Butte sediments of western Nebraska, equids are represented by anchitheriines and brachyodont parahippines, and no merychippines are present. Therefore, the Box Butte Formation represents an important time interval in the midcontinent, that records the apparently simultaneous first occurrence of at least three relatively primitive merychippines. They appear to be at the base of the series of cladogenetic events that resulted in the radiation of hypsodont horses.

Although many species of *Merychippus* s.l. have been named from southern California, most are of late Barstovian age and are derived relative to the *Parahippus-Merychippus* transition. However, two small, late Hemingfordian species have been described, "*M.*" *carrizoensis* and "*M.*" *tehachapiensis* (Dougherty, 1940; Buwalda and Lewis, 1955). Munthe (1979) analyzed other collections from California (the Vedder Creek l.f.), and concluded that "*M.*" *carrizoensis* was the senior synonym of "*M.*" *tehachapiensis.* He also provided comparisons with coeval Sheep Creek merychippines, especially "*M.*" *primus.* Quinn (1984) described for the first time the cranial morphology of "*M.*" *carrizoensis,* and stressed its equine characteristics.

In a new attempt to separate the paraphyletic merychippines and hipparionines into monophyletic groups, Skinner and MacFadden (1977) erected a new genus, *Cormohipparion,* and included the derived configuration of the DPOF as a diagnostic character. MacFadden and Skinner (1981, 1982) referred the new early Barstovian species *C. goorisi* to *Cormohipparion,* as it shares with younger taxa distinctive features of the DPOF, although it is dentally at a primitive merychippine grade of evolution. This evolutionary character mosaic led Forstén (1982) to take issue with the validity of the genus *Cormohipparion,* and the inclusion of *C. goorisi.* She argued that it merely was a member of the merychippine complex (see response by MacFadden and Skinner, 1982).

Honey and Izett (1988) referred a poorly

preserved skull with very heavily worn teeth from the Browns Park Formation, Moffat County, northwestern Colorado, to *Parahippus* cf. *P. leonensis*. The condition of the skull and teeth makes specific (and even generic) level identification hazardous, but the size of the specimen, and the configuration of the DPOF argue against an especially close relationship with "*P.*" *leonensis*. The toothrow length (UTRL) of the specimen is reported to be 99.4 mm; compensating for the normal decrease in length associated with ontogenetically advance wear produces an estimated UTRL of 105 to 110 mm in the moderate wear stage. This is about 15 percent greater than Thomas Farm "*P.*" *leonensis*, and at least 10 mm more than the maximum observed value of 95.6 mm. The DPOF appears to be much better defined and have a wider preorbital bar (Honey and Izett, 1988: fig. 10) than those described below from Thomas Farm. This specimen, like the skull mentioned above from the Box Butte Formation that was listed by Galusha (1975) as near *P. vellicans*, must be removed from possible consideration as a northern representative of "*P.*" *leonensis*.

With the now widespread acceptance of cladistic methodology, the complex systematics of fossil horses are well suited for this type of analysis. An earlier study was done on Eocene equids (MacFadden, 1976), but only recently have workers begun to tackle the complex phylogeny at the base of the Miocene radiation. Evander (1989) rigorously analyzed 33 dental and postcranial characters for 19 of the principal genera of the Equidae. For each of these, he used a single, well-known representative species for character analysis, determined polarities, and constructed a cladogram and phylogeny. Sheep Creek "*M.*" *primus* was used for the genus *Merychippus*. Hulbert (1989) presented a cladistic analysis of 10 species of merychippine grade and 13 Late Neogene genera using 45 characters (five autapomorphic for terminal taxa). Several most parsimonious arrangements of the taxa were found, of which one was selected as the evolutionarily most likely scenario. Both studies concluded that *Merychippus* as traditionally employed by Stirton (1940), Simpson (1951), or Forstén (1975) is an artificial, paraphyletic assemblage. The essential patterns derived from these two studies are similar to those presented below, but were based both on fewer merychippine-grade taxa and far fewer characters relevant to merychippines. This study differs from Hulbert (1989) in that many more multistate characters are employed, and all character states were obtained from actual specimens rather than the literature. For these reasons the hypotheses presented here are preferred over those of Evander (1989) or Hulbert (1989) to the extent that they differ.

MATERIALS AND METHODS

Hemingfordian and Barstovian equids from the following collections were examined: AMNH, F:AM, MCZ, TMM, UF, and UF/FGS. Twelve merychippine-grade species were selected for analysis: "*Merychippus*" *gunteri*, "*M.*" *primus*, "*M.*" *tertius*, "*M.*" *carrizoensis*, "*M.*" *intermontanus*, *Protohippus vetus*, *Pliohippus mirabilis*, "*Merychippus*" sp. cf. "*M.*" *sejunctus*, "*M.*" *coloradense*, *M. insignis*, "*M.*" *goorisi*, and *Hipparion shirleyae* (see descriptions below). For reasons detailed below, the superb sample of "*Parahippus*" *leonensis* from Thomas Farm was chosen as the outgroup for the analysis. Character states were observed and recorded for each taxon (table 1) and, whenever allowed by sufficient sample sizes, numerous specimens were examined to check for variation in character expression. For characters with minor amounts of intraspecific variation, the state reported in table 1 is the one observed in the majority of specimens. Measuring regimens for crania, mandibles, and postcranial elements were devised that correspond to those of Eisenmann (1986). The measuring phase of this study was completed prior to the publication of Eisenmann et al. (1988), which presented a standardized measuring regimen for equids. Most but not all of the measurements of Eisenmann (1986) directly correspond to those of Eisenmann et al. (1988). Dental measurements correspond to those of Hulbert (1987, 1988a). The character matrix was phylogenetically analyzed following the procedures outlined on p. 40. The recent review of Miocene mammalian biochronology by Tedford et al. (1988) pro-

vided a chronological framework for the analysis.

Characters and Character States

Based on a review of previous literature and our own observations of fossil equids, nearly 100 characters were selected for incorporation into this and our future phylogenetic studies. Many of these are traditional and do not require detailed description. Most of the postcranial characters were taken from the anatomical syntheses of Sondaar (1968) and Hussain (1975); additional characters mentioned by these authors were judged to be too subject to intraspecific variation, or of use only in distinguishing *Equus* from other equids. Of these characters, only 39 had differing character states between the outgroup and two or more of the selected ingroup taxa. The remainder either exhibited the same character state in all 13 of the analyzed taxa (when known), or had a single occurrence of a derived (autapomorphic) state among the 12 ingroup taxa. These were deleted from the PAUP analysis, as they do not provide information concerning interrelationships. Quantitative characters with three or more states were considered to be transformational morphocline sequences. We list below the utilized characters by a standard numbering scheme that is consistent with our other phylogenetic studies (e.g., Hulbert, 1988c; and work in progress). The observed character states found in each of the taxa under study are listed in table 1.

While most workers in the field would agree that the selected characters have systematic utility, our choices as to the number of states per character and their definitions require some comment. Although some characters may seem to be too finely partitioned, the expressed magnitude of morphological difference between adjacent states is the same as, or very similar to, those we have used as species-level differentia in numerous previous studies. Thus the utility of many of the states has been proven empirically. Conversely, some character states may appear to be too broadly defined and thus mask potentially useful systematic information. Broad definitions were necessary in some cases because species or clades exhibit differing degrees of intraspecific variation for some characters. For these, character state limits had to be based on the level of variation in the most variable taxon. Broadly defined character states also resulted if discernible morphological gaps among the taxa were widely spaced (see below). Many phylogenetically important changes in the dentitions of equids do not involve the simple presence/absence of characters, but rather the relative wear stage during which a character state is expressed or lost on the occlusal surface (Hulbert, 1987). Thus many of our dental characters depend on the relative persistence (as defined above) of a particular feature. This should optimally result from detailed quantitative study of numerous individuals of various wear stages (e.g., Webb and Hulbert, 1986: fig. 3). For all of the taxa under study here such samples are lacking, except for "*P.*" *leonensis* and "*M.*" *primus* (and to a lesser extent *Pliohippus mirabilis*). When and if larger samples of the other taxa become available, analytical study may demonstrate that some of our estimates were slightly inaccurate, but we do not anticipate significant changes to our results.

Boundaries for character states of quantitative characters were chosen on the basis of observed ranges of variation, and, as often as possible, the principles used in gap-coding (Archie, 1985; Goldman, 1988). This means that boundaries between states are placed at observed morphological discontinuities along a quantitative continuum. The result is that the morphology observed in the majority of individuals of a species falls within a single character state. Generalized gap-coding using the methods of Goldman (1988) was attempted for three quantitative characters (numbers 7, 16, and 70 below), but available sample sizes were small ($N < 5$) in the majority of taxa for these and other characters. Therefore the estimated sample means and standard deviations used in this procedure for these characters were subject to the vagaries of ontogenetic and individual variation, and lacked the accuracy needed for this type of analysis. We thus chose not to use Goldman's gap-coding methods in these cases. Gap-coding routinely resulted in many more character states than we recognize. For a few characters, notably 71 (unworn molar crown height), the continuum of observed

TABLE 1

Character State Matrix for Merychippine Equids

(Characters and character states are defined in the text on pp. 17–19. A "?" indicates an unknown state due to lack of material; these were treated as missing states in the PAUP analysis.)

	Characters																			
	2	3	5	6	7	8	12	15	16	20	21	23	27	28	29	30	31	32	33	35
"*P.*" *leonensis*	0	1	0	0	0	0	0	0	2	0	0	0	4	4	0	1	0	0	3	1
"*M.*" *gunteri*	?	?	?	?	?	?	?	?	?	1	1	0	4	4	0	2	1	0	3	1
"*M.*" *primus*	0	1	0	0	0	0	0	0	2	1	1	1	2	1	1	2	1	0	2	1
"*M.*" *tertius*	1	2	1	0	0	1	1	0	1	1	2	1	3	2	1	2	2	0	2	1
"*M.*" *carrizoensis*	1	3	3	0	0	1	2	?	3	1	1	1	0	0	1	1	1	0	1	1
P. vetus	?	?	?	?	?	?	?	?	?	1	2	2	2	1	1	2	1	0	2	1
"*M.*" *intermontanus*	1	3	2	0	1	0	0	0	2	2	2	2	2	2	1	2	1	0	2	1
"*M.*" *coloradense*	1	2	2	0	0	0	0	0	2	?	2	2	4	4	1	2	2	0	3	2
M. insignis	1	2	2	0	1	0	0	0	2	1	2	1	4	4	1	3	2	1	4	2
"*M.*" *goorisi*	1	3	3	1	1	0	0	0	2	1	2	1	5	5	1	3	2	1	5	2
"*M.*" cf. *sejunctus*	1	2	1	0	0	0	1	0	2	?	2	1	1	2	1	2	2	0	3	1
P. mirabilis	1	3	3	1	1	0	2	0	2	2	2	1	0	0	2	1	1	0	1	1
"*H.*" *shirleyae*	1	2	1	1	2	0	0	0	2	1	2	2	4	4	1	2	2	0	4	0

	38	39	40	41	43	45	48	52	54	55	56	57	62	63	66	67	70	71	79
"*P.*" *leonensis*	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0
"*M.*" *gunteri*	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	1	1	?
"*M.*" *primus*	2	2	0	0	0	1	0	0	0	1	1	1	1	0	0	0	1	1	?
"*M.*" *tertius*	2	2	0	0	0	2	0	0	1	1	1	1	1	0	0	0	2	2	1
"*M.*" *carrizoensis*	2	2	1	0	0	1	0	0	1	1	1	1	1	0	0	1	1	1	?
P. vetus	2	2	0	0	1	?	2	1	1	1	1	1	1	1	1	1	2	3	?
"*M.*" *intermontanus*	2	2	1	1	1	2	?	1	1	1	1	1	1	0	1	1	2	3	?
"*M.*" *coloradense*	2	1	1	0	1	2	?	1	1	2	1	1	2	1	0	0	3	4	1
M. insignis	1	1	1	1	0	2	2	1	1	2	1	1	1	0	0	0	2	3	?
"*M.*" *goorisi*	0	0	0	0	0	2	2	2	1	2	1	1	1	0	0	0	2	3	?
"*M.*" cf. *sejunctus*	2	2	0	0	0	2	?	1	1	2	1	1	1	0	0	0	2	4	?
P. mirabilis	3	3	1	1	0	2	0	0	1	1	1	1	1	1	1	1	3	6	0
"*H.*" *shirleyae*	1	1	1	0	0	2	1	1	1	2	1	1	1	0	0	0	1	3	1

morphology had to be subdivided arbitrarily as statistical data to formulate gaps were lacking. In these cases the magnitude of each state was chosen to be equivalent to the average sample variance. Potentially, a taxon could be assigned a different character state than that given to a species it closely resembles (because of the arbitrary subdivisions). Therefore we have tried to minimize the use of such characters.

The following list provides descriptions of the characters and character states used in this analysis. The numbers used to refer to characters are not sequential so as to conform with those used in other studies.

2. Frontal Bones. Two states are recognized: 0, frontal bones notably domed; 1, frontal bones flat, not domed.
3. Depth of DPOF. The DPOF is a depression of varying depth and morphology present in many fossil equids. Four states are recognized: 0, fossa absent or very rudimentary; 1, depth of fossa relative to the surrounding surface of the skull very shallow, maximum depth less than 5 mm; 2, depth shallow, about 5–10 mm; 3, depth moderate, 10–15 mm.
5. DPOF Posterior Margin and Pocket. Four states are recognized: 0, posterior margin of DPOF without a pronounced rim, no pocket; 1, posterior margin with a pronounced rim, but not pocketed; 2, posterior margin with rim and shallow pocket, less than 5 mm deep; 3, posterior margin with rim and pocket depth greater than 5 mm. By a pronounced rim we mean that the margin of the fossa is very easily discernible because of a distinct change in slope.
6. Distinct Ventral Rim on DPOF. Two states are recognized: 0, ventral rim of DPOF without distinct or pronounced margin; 1, ventral rim distinctly rimmed.
7. Relative Preorbital Bar Length. The preorbital bar length is the distance between the orbit and the DPOF. Relative preorbital bar length is determined by dividing it by UTRL. Three states are recognized: 0, narrow (ratio < 0.10); 1, moderate (ratio 0.10 to 0.20); 2, long (ratio >0.20).
8. DPOF Shape. Two states are recognized: 0, elongate-oval (length much greater than height); 1, oval (length about equal to height).
12. Malar Fossa. In addition to a DPOF, some equids have a depression in the ventral preorbital region termed a malar fossa. Three states are recognized: 0, no malar fossa present; 1, rudimentary or shallow malar fossa present (<10 mm deep); 2, deep malar fossa present (>10 mm deep).
16. Relative Muzzle Length. Character state is determined by comparison of upper P2-I3 diastema length (UDL) and UTRL in middle age adults. Four states are recognized: 0, short (UDL <40% of UTRL); 1, moderate (UDL between 40 and 55% of UTRL); 2, elongated (UDL between 55 and 70% of UTRL); 3, very elongated (UDL >70% of UTRL).
20. Cement on Deciduous Premolars. Three states are recognized: 0, no cement present; 1, cement layer rudimentary and very thin (<1 mm thick), commonly only found on DP4 and dp4; 2, moderate to very thick coating (>1 mm thick) of cement on all deciduous cheekteeth.
21. Cement on Permanent Cheekteeth. Three states are recognized: 0, thin layer of cement present, <1 mm in thickness; 1, moderate layer of cement present, about 1 mm thick; 2, thick (>1.5 mm) layer of cement present, as in *Equus*.
23. Protocone Shape (P3-M2). Based on average value of ratio of protocone length (PRL) to width (PRW), taken in moderate wear stages. Three states are recognized: 0, round (ratio <1.2); 1, oval (ratio 1.2–2.0); 2, elongate-oval (ratio 2.0–3.0).
27. Timing of Protocone Connection to Protoloph on the P3 and P4. Six states are recognized: 0, protocone connected to protoloph immediately after onset of occlusal wear; 1, connected during the very early wear stage; 2, connected during the early wear stage; 3, connected during the early moderate wear stage; 4, connected during the late moderate wear stage; 5, connected during the late wear stage.
28. Timing of Protocone Connection to Protoloph on the M1 and M2. Same six states as character 27.

29. Protocone Connection to Hypocone on the M1 and M2. Three states are recognized: 0, protocone never connects to hypocone; 1, connection occurs only in late wear stage; 2, connection occurs prior to late wear stage.
30. Pli Caballin on P2-P4. Four states are recognized: 0, pli caballin absent or very rare; 1, pli caballin common, but small (<2 mm) and nonpersistent; 2, pli caballin well developed, relatively persistent, commonly single or unbranched; 3, pli caballin well developed, commonly branched or multiple.
31. Pli Caballin on M1-M3. Same four states as character 30.
32. External Fossette Plications. Two states are recognized: 0, pli protoloph and pli hypostyle rare, or if present single and nonpersistent; 1, pli protoloph and/or pli hypostyle common, persistent, but single.
33. Internal Fossette Plications. This character is based on the common fossette morphology observed in early and moderate wear stages. Six states are recognized: 0, all internal fossette plications (pli prefossette, pli postfossette, etc.) absent, or very rare (if present simple, shallow, and nonpersistent); 1, very simple internal fossette plications (pli prefossette and pli postfossette single or absent, can be deep, prefossette loop not prominent); 2, simple but nonpersistent internal fossette plications (pli prefossette and pli postfossette multiple in early wear stages, single in moderate wear stages, absent in late wear stages) that are shallow and nonbranching; 3, simple but persistent internal fossette plications (as in 2 but with plications generally present in later wear stages); 4, moderately complex internal fossette plications (2 to 5 plications present on each side in early and moderate wear stages, with a limited amount of branching); 5, complex internal fossette plications (3 to 7 plications present on each side in early and moderate wear stages, branching of plications common).
35. Metastyle Development. Three states are recognized: 0, metastyle generally absent or very weak; 1, metastyle common but not strong (e.g., fig. 7A–H); 2, metastyle very well developed (e.g., fig. 7I, especially the P3 and M2).
38. Timing of Hypoconal Groove Closure on P2-P4. Four states are recognized: 0, hypoconal groove open to near the base of the crown; 1, hypoconal groove closed in late wear stages; 2, hypoconal groove closed in moderate wear stages; 3, hypoconal groove closed in early wear stages.
39. Timing of Hypoconal Groove Closure on M1-M2. Same four states as character 38.
40. Hypoconal Lake on P3-P4. Two states are recognized: 0, hypoconal groove does not form an isolated lake when it closes; 1, hypoconal groove does form a lake after closing.
41. Hypoconal Lake on M1-M2. Same two states as character 40.
43. Curvature of Upper Cheekteeth (P3-M2). Based on the radius of curvature (ROC) measured along the mesostyle (Skinner and Taylor, 1967). Two states are recognized: 0, strongly curved, ROC <40 mm; 1, moderately curved, ROC from 40 to 70 mm.
45. Retention of the dp1. Three states are recognized: 0, dp1 relatively large, commonly retained with permanent dentition; 1, dp1 very reduced (diameter <2 mm), variably present with adult dentition; 2, dp1 very rarely present with permanent dentition; vestigial if present.
48. Strength of Protostylids on dp3-dp4. Three states are recognized: 0, protostylids weak, may be present only near base of crown as the anterior cingulum, and not appear on the occlusal surface until late wear stages; 1, protostylids moderately well developed, positioned in anterolabial corner of the tooth, appear in early wear stage (e.g., p3 and m1 in fig. 8J); 2, protostylids very well developed, extend labially about as far as the protoconid, straight (e.g., fig. 9H).
52. Strength of Protostylids on p3-m3. Same three states as character 48.
54. Expansion of Metaconid-Metastylid Complex. Two states are recognized: 0, metaconid-metastylid relatively small and unexpanded (mml of p3 or p4 av-

erages ≤ 45% of apl); 1, metaconid-metastylid expanded but not elongated (mml of p3 or p4 averages between 45 and 50% of apl).

55. Separation of Metaconid and Metastylid on p3-m3. Three states are recognized: 0, metaconid and metastylid not well separated from one another even in very early wear stages; 1, well separated from each other only in very early and early wear stages; 2, persistently well separated from each other. Well separated means that the areas of exposed dentine of the metaconid and metastylid are distinctly separated from each other by the linguaflexid, ectoflexid, metaflexid, and entoflexid, with only a narrow passage of dentine connecting them.
56. Metaconid-Metastylid on p2. Two states are recognized: 0, single median lingual cuspid present, not separated into metaconid and metastylid (fig. 8A–C); 1, separate metaconid and metastylid present on p2, at least in early wear stage.
57. Development of Pli Entoflexid. Two states are recognized: 0, pli entoflexid absent or rudimentary; 1, pli entoflexid commonly present, at least in early and very early wear stages.
62. Ectoflexid Depth on p2. Three states are recognized: 0, ectoflexid deep, completely penetrates isthmus; 1, ectoflexid moderately deep, only partially penetrates isthmus; 2, ectoflexid shallow, does not penetrate isthmus.
63. Ectoflexid Depth on p3-p4. Same three states as character 62.
66. Relative Size of Metaconid and Metastylid on p3-p4. Two states are recognized: 0, metaconid and metastylid equal or subequal in size; 1, metastylid notably smaller than metaconid and located more lingually.
67. Relative Size of the Metaconid and Metastylid on m1-m3. Two states are recognized: 0, metaconid and metastylid equal or subequal in size and position of their lingual borders; 1, metastylid notably smaller than metaconid, lingual border located more labially than that of metaconid especially in moderate and late wear stages.
70. Toothrow Length. This character is used as an indicator of overall size, and reflects the mean UTRL in moderate wear stage. Four states are recognized: 0, less than 90 mm; 1, about 90 to 105 mm; 2, about 105 to 125 mm; 3, about 125 to 140 mm.
71. Unworn Molar Crown Height. This character is determined by unworn M1 mesostyle crown height or m1 metaconid crown height, ±2.5 mm. Seven states are recognized: 0, less than 22 mm; 1, about 25 mm; 2, about 30 mm; 3, about 35 mm; 4, about 40 mm; 5, about 45 mm; 6, about 50 mm.
79. Articulation of the MC V. Two states are recognized: 0, MC V articulates primarily on the unciform, articulation facet for MC IV absent or smaller than that for unciform; 1, MC V articulates primarily on the MC IV, articulation facet for unciform absent or smaller than that for MC IV.

Description of Analyzed Taxa

Species were included in this study if they fulfilled at least two to the following three criteria: (1) it was at or near the base of the adaptive radiation of the Equinae (i.e., of Hemingfordian or early Barstovian age); (2) it was a member of an otherwise unrepresented clade within the merychippine radiation, as determined from previous studies (Hulbert, 1988c, 1989); and (3) it was represented by a good morphological sample, to allow confident character state determination for most of the characters. Our minimum requirements for the latter were the availability of both permanent and deciduous, upper and lower cheekteeth from individuals of differing wear stages. The availability of a skull or postcranial elements outweighed the absence of deciduous cheekteeth. Merychippine-grade taxa eliminated by these criteria are "*M.*" *stevensi,* "*M.*" *relictus,* "*M.*" *seversus,* "*M.*" *stylodontus, M. brevidontus, M. californicus, M. calimarius,* "*M.*" *republicanus,* and ?*Calippus circulus.* With these exceptions the study includes all recognized late Hemingfordian and early Barstovian merychippines (or, in case of "*M.*" *isonesus,* its presumed anagenetic predecessor, "*M.*" *tertius*). Most of these fail the third criterion

listed above, and are known from too few characters for their phylogenetic relationships to be determined accurately. In this section we present the type status and referred samples, temporal and paleobiogeographic distribution, and brief descriptions of new material or characters for the 13 included taxa. We do not, however, provide a complete synonymy or extensive morphological descriptions; both are beyond the scope of the current study, and in most cases the latter can be found in the older literature or in table 1. This study is not intended to be, nor should it replace, a traditional taxonomic survey of these species. Listed for each taxon are the samples we personally observed to compile the matrix of character states; only rarely was the previous literature used, except to confirm our observations.

"*Parahippus*" *leonensis* Sellards, 1916

TYPE SPECIMEN AND LOCALITY: FGS 5084, R M1 or M2, collected from Griscom Plantation, early (?) Hemingfordian, Leon County, Florida. The holotype was not in the FGS collection when it was transferred to UF, and is apparently lost. It was not given to the USNM as were several of the older FGS type specimens. The topotypic sample comprises in addition only fragments of cheekteeth and a few postcranial elements. The holotype was well illustrated by Sellards (1916) and Osborn (1918), and we do not feel there is sufficient need at this time to erect a neotype (cf. Article 75 in Ride et al., 1985).

MATERIAL STUDIED: (1) A large sample contained in the UF, UF/FGS, MCZ, and F:AM collections from the late early Hemingfordian Thomas Farm l.f., Gilchrist County, Florida which formed the major basis for morphological analysis of this species. Five relatively complete crania, UF 43613, 44778, 56000, 103753, and UF/FGS V-6604, were used to determine facial and other cranial character states. Simpson (1932), White (1942), and Hulbert (1984) provided illustration of material from this locality. (2) A limited sample of teeth and postcranial elements from the Seaboard Airline Railroad Site, Leon County, Florida (UF/FGS collection). (3) Although not studied in great detail here, we follow White (1942) and Forstén (1975) who referred the topotypic sample of "*Parahippus*" *vellicans* from the early Hemingfordian Garvin Farm l.f. of the eastern Texas Gulf Coastal Plain to "*P.*" *leonensis* (TMM, TAMU collections). (4) An associated skull, mandible, and partial skeleton, F:AM 109357, from Marshall Ranch (early Hemingfordian, Runningwater Formation), Dawes County, Nebraska, provisionally referred here to "*P.*" *leonensis*. It is the only specimen unequivocally at the "*P.*" *leonensis*-grade of dental evolution known to us from pre-Barstovian deposits beyond the Gulf Coastal Plain.

DISTRIBUTION: Late early Hemingfordian of Florida, Texas, and Nebraska (ca. 18 to 19 Ma).

DISCUSSION: Previous descriptions and discussions of "*P.*" *leonensis* (e.g., Simpson, 1932; White, 1942; Forstén, 1975) dealt mostly with dental characters. These authors and others (Schlaikjer, 1937; Downs, 1956) have demonstrated that "*P.*" *leonensis* is one of the dentally most advanced parahippines, having such character states as relatively high crowned teeth, presence of cement, well-developed crochet often with pli caballin, plicated metaloph, absence of lingual cingula on permanent upper cheekteeth, absence of labial cingula on permanent lower cheekteeth, and relatively distinctly separated metaconids and metastylids on p3-m3. Most of these are synapomorphies uniting "*P.*" *leonensis* and the 12 other taxa under study here. A few other described parahippines (*P. avus, P. cognatus, P. coloradensis*) share some of these characters, but they are known only from the Barstovian. At least 4 of the 12 ingroup merychippines are of late Hemingfordian age, implying that their closest sister taxon should be of a comparable or older age. "*Parahippus*" *leonensis* is thus the best taxon to use as an outgroup for an analysis of merychippines for three reasons: (1) it shares with them numerous derived dental character states not observed in anchitheriines, *Archaeohippus,* Paleogene equids, and the majority of parahippines; (2) it is of sufficient age to be ancestral or contemporaneous with all of the ingroup taxa; and (3) it is extremely well represented by a quarry sample of sufficient size

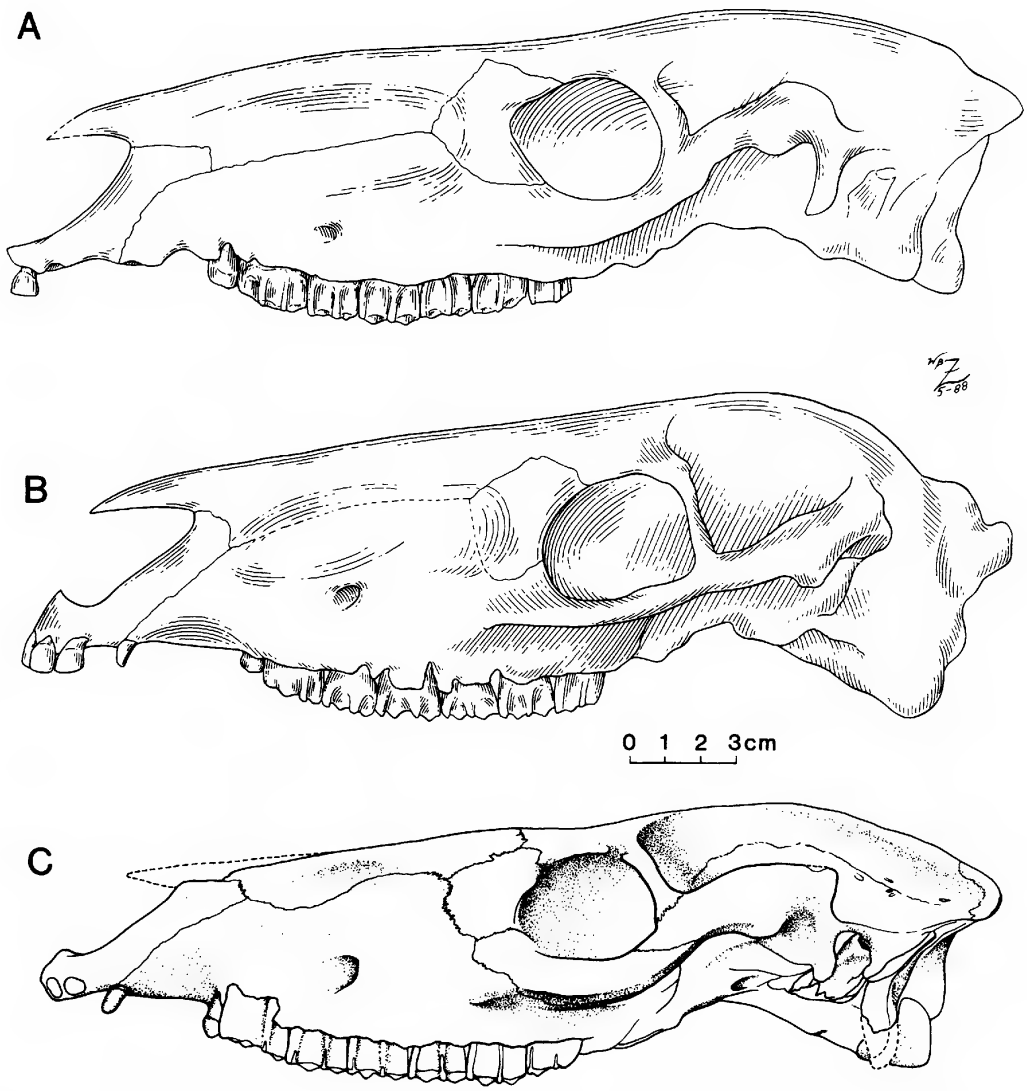
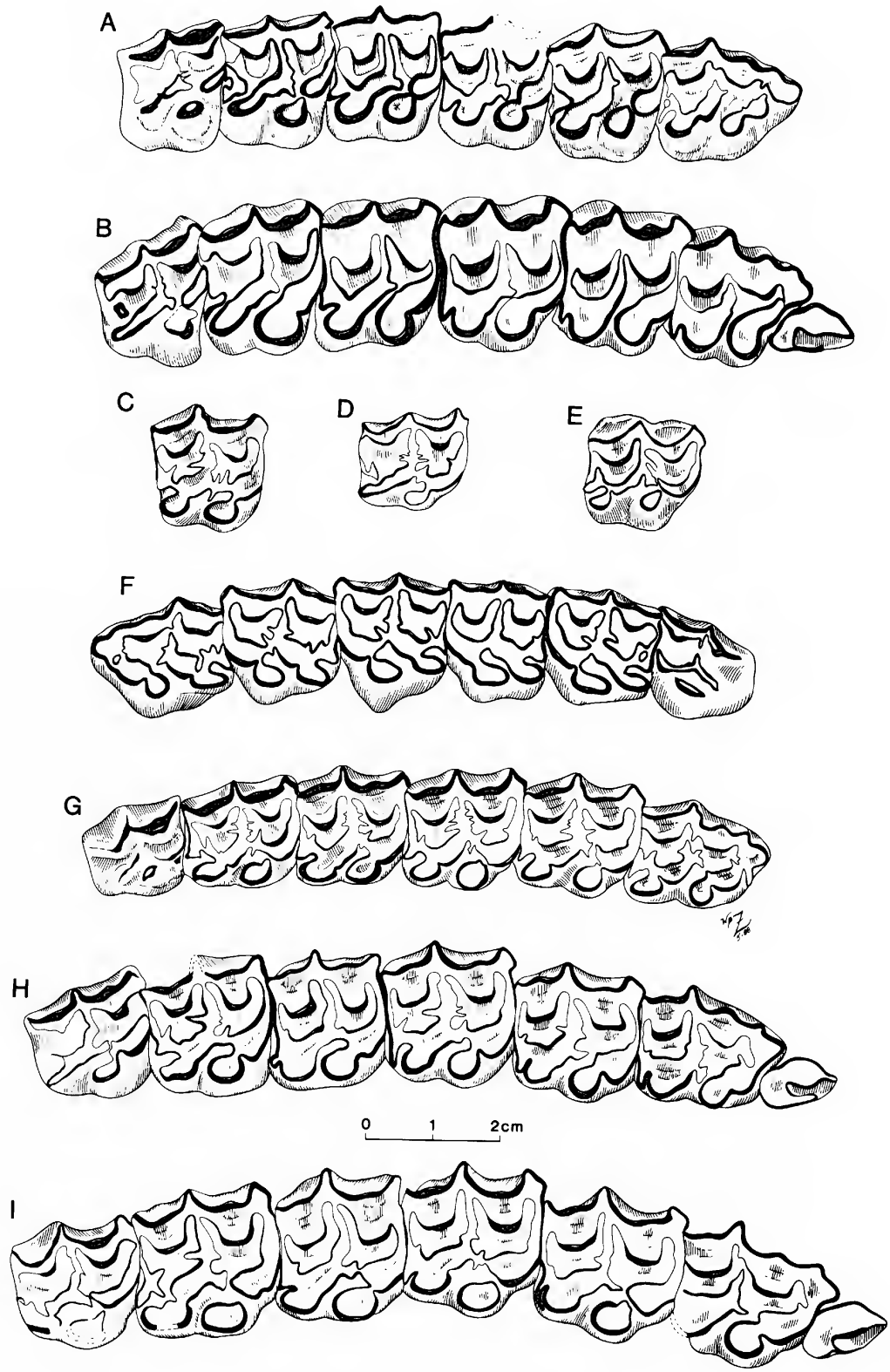


Fig. 6. Lateral views of crania of Hemingfordian Equinae. **A.** "*Parahippus*" *leonensis,* Thomas Farm, Gilchrist County, Florida (late early Hemingfordian). Composite based on UF 56000 and UF 103753. **B.** F:AM 109857, "*P.*" *leonensis,* Marshall Ranch, Dawes County, Nebraska (early Hemingfordian). Upper cheekteeth of this individual illustrated in figure 7B; lower cheekteeth in figure 8B. **C.** F:AM 69700, "*Merychippus*" *primus,* Greenside Quarry, Sheep Creek Fauna, Sioux County, Nebraska (late Hemingfordian). Upper cheekteeth of this individual illustrated in figure 7F.

to determine character states and variation for every skeletal element.

With the exception of isolated teeth and dense carpal and tarsal elements, most specimens from Thomas Farm were affected by postburial compaction. Skulls in particular were subjected to a great deal of crushing. However, a number of relatively complete skulls, although crushed to varying degree, have accumulated over the years, and these now permit a description of cranial features that have been omitted from previous studies. There is no malar fossa or depression in the ventral preorbital region (fig. 6A). The DPOF is a relatively large, but very shallow, oval depression with very poorly defined borders and no posterior pocket. The preorbital bar is short, between 3 and 4 mm. Mean


A
B
C
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muzzle width is 32.2 mm (OR = 28.7–35.4; N = 3); this amounts to about 35 percent of mean UTRL (92.0 mm). That is within the range of normal or baseline values for relative equid muzzle width (Hulbert, 1988a). The two specimens with the least amount of dorsal-ventral crushing, UF 56000 and UF 103753, demonstrate that the frontals of "*P.*" *leonensis* are notably domed like those of "*Merychippus*" *primus* (fig. 6A, C). The nasal notch is not deeply retracted; at its deepest point it approximately overlies the mid-point of the postcanine diastema.

The Nebraska specimen (F:AM 109357) considerably extends the geographical range of "*Parahippus*" *leonensis,* as the taxon was previously known only from the Gulf Coastal Plain (excluding the heavily worn skulls referred by Galusha, 1975, and Honey and Izett, 1988, that we regard as specifically undiagnostic). F:AM 109357 (figs. 6B, 7B, 8B; tables 2, 3) from the early Hemingfordian Runningwater Formation of Nebraska closely resembles referred specimens of "*P.*" *leonensis* from Thomas Farm, and especially indivuals from the Garvin Farm l.f. of Texas. Its most important features are: the cemented, relatively hypsodont cheekteeth; well-developed crochet; and absence of cingula on the lingual side of the upper cheekteeth and labial side of the lower cheekteeth. Its cranial characters conform in every detail to those described above for Thomas Farm specimens (fig. 6A, B). In terms of size, F:AM 109357 falls within the observed range of measured dental, cranial, and postcranial characters of the Thomas Farm sample (tables 2, 3). Differences from typical members of the Thomas Farm "*P.*" *leonensis* population include the relatively thin coating of cement, absence of pli caballin, and relatively simple fossette margins (fig. 7A, B). However, some Florida specimens, and proportionally more of the Texas specimens also share these "primitive" traits. We agree with Forstén (1975) that the slight differences between the older Garvin Farm and younger Thomas Farm populations are probably chronoclinal, and infer that the Runningwater specimen also represents a chronologically older individual of the same species, perhaps as much as 0.5 m.y. older than Thomas Farm. F:AM 109357 is the only Runningwater specimen from the F:AM and AMNH collections referable to "*P.*" *leonensis*; all the other parahippines from that horizon have much more primitive dentitions. It demonstrates that dentally advanced parahippines were not limited to the Gulf Coastal Plain during the early Hemingfordian, and provides a relatively undistorted cranium for this taxon.

"*Merychippus*" *gunteri* Simpson, 1930

TYPE SPECIMEN AND LOCALITY: UF/FGS V-4114, R P3 or P4, from the late Hemingfordian Midway l.f., Torreya Formation, Gadsden County, Florida.

MATERIAL STUDIED: (1) The topotypic sample of this species, housed in the UF/FGS and AMNH collections (listed in table 4). Also a few isolated teeth from the stratigraphically equivalent Quincy l.f. (2) A sample of mostly isolated teeth from the Burkeville and Cold Spring Faunas, Barstovian of the Texas Gulf Coastal Plain in the TMM and TAMU collections (listed by Forstén, 1975: 22–23).

DISTRIBUTION: Late Hemingfordian to early Barstovian of Florida; earliest Barstovian to very early late Barstovian of Texas (ca. 14 to 18 Ma).

←

Fig. 7. Occlusal views of upper cheekteeth of Hemingfordian Equinae from Florida and Nebraska. **A.** UF 100012, "*Parahippus*" *leonensis,* Thomas Farm, Gilchrist County, Florida. Associated right P2-M3. **B.** F:AM 109857, "*P.*" *leonensis,* Marshall Ranch, Dawes County, Nebraska. Right DP1-M3. C–E. "*Merychippus*" *gunteri,* Fuller's Earth Company Mine (Midway l.f.), Gadsden County, Florida. **C.** UF/FGS V-4114, right P3 or P4 (holotype). **D.** UF/FGS V-5045, left (reversed) P4. **E.** UF/FGS V-9952, right DP3 or DP4. **F.** F:AM 69700, "*M.*" *primus,* Greenside Quarry, Sioux County, Nebraska. Left P2-M3. **G.** F:AM 125573, "*M.*" *primus,* Sand Canyon, Box Butte Formation, Dawes County, Nebraska. Right P2-M3. **H.** F:AM 125586, "*M.*" *tertius,* Foley Quarry, Box Butte Formation, Box Butte County, Nebraska. Right DP1-M3. **I.** F:AM 125596, indeterminant large merychippine, Foley Quarry, Box Butte Formation, Box Butte County, Nebraska. Left (reversed) DP1-M3.

TABLE 2

Cranial and Dental Measurements of Hemingfordian Equids

[Comparison of measurements of F:AM 109857, a referred female specimen of "*Parahippus*" *leonensis* from the Runningwater Formation, Dawes County, Nebraska, with the sample statistics ($\bar{x}$, *s*, OR, N) of the referred "*P.*" *leonensis* population from the Thomas Farm l.f., Gilchrist County, Florida, and the "*Merychippus*" *primus* population from Thomson Quarry, Sheep Creek Fauna, Sioux County, Nebraska. The values for F:AM 109875 fall within the OR of the Thomas Farm sample for almost all measurements, and differ with those of the "*M.*" *primus* sample when the two species differ (e.g., lower tooth width, height of IOF). The number in parentheses refers to the same measurement used by Eisenmann (1986). An "a" before a measurement indicates an approximate value due to breakage, crushing, or water wear. All determinations in mm. Comparisons are made between similar wear classes for the dental characters (moderate wear stage for P2-M2 and p2-m2, and early wear stage for M3 and m3), and individuals of the same sex (female) for canine dimensions.]

	F:AM 109857	"*P.*" *leonensis*	"*M.*" *primus*
Skull			
Basilar length (1)	236	236	239.6, 5.05, 233.0–248.5, 6
Facial length	176	—	177.3, 6.14, 170.0–187.5, 8
P2-P4 length (7)	49.8	48.7, 2.39, 45.0–51.1, 5	50.8, 0.89, 49.4–51.9, 7
M1-M3 length (7b)	42.8	43.8, 2.02, 40.5–46.5, 6	43.7, 1.46, 41.4–45.9, 8
P2-M3 length (8)	91.1	92.0, 4.39, 84.6–95.6, 5	93.9, 1.88, 92.3–97.8, 6
I3-P2 diastema L (6)	46.8	46.1, 3.41, 42.6–50.1, 4	44.0, 3.56, 37.9–50.4, 15
Muzzle width (17)	29.8	32.3, 3.39, 28.7–35.4, 3	33.5, 1.35, 31.2–36.8, 16
Canine length	4.1	5.0	4.3, 0.35, 3.9–4.8, 7
Canine width	3.5	3.4	3.0, 0.23, 2.6–3.5, 8
IOF height	23.0	22.2, 2.07, 20.1–24.4, 4	26.7, 2.14, 23.8–33.8, 22
DPOF length	a67	—	70.2, 3.39, 64.6–76.2, 8
DPOF height	a26	—	23.1, 2.51, 19.0–26.3, 7
Preorbital bar length	a5	3.7	4.8, 1.07, 3.0–6.0, 9
P2			
MSCH	6.6	8.3, 1.81, 4.2–12.6, 34	15.3, 11.2–18.8, 28
APL	18.8	19.2, 0.87, 16.9–21.0, 32	19.7, 0.77, 18.2–21.4, 28
TRW	16.9	15.4, 1.11, 13.3–17.5, 32	15.7, 0.90, 13.6–17.1, 28
PRL	4.8	3.9, 0.48, 2.9–4.9, 34	4.1, 0.28, 3.4–4.5, 28
PRW	5.4	4.4, 0.66, 3.6–5.7, 34	4.1, 0.38, 3.4–4.7, 28
P3			
MSCH	6.9	8.8, 2.22, 4.7–12.3, 12	14.8, 8.8–21.9, 18
APL	15.5	16.2, 0.92, 13.6–17.4, 12	16.6, 1.08, 14.8–18.9, 24
TRW	18.2	17.4, 1.39, 14.8–19.3, 12	17.7, 0.68, 15.6–18.7, 24
PRL	4.9	4.6, 0.43, 4.1–5.7, 12	5.1, 0.44, 4.1–6.1, 24
PRW	6.1	4.5, 0.67, 3.6–5.4, 12	4.5, 0.54, 3.6–5.7, 24
P4			
MSCH	6.5	7.2, 2.25, 4.1–10.8, 12	13.7, 8.1–21.4, 18
APL	16.1	15.9, 0.89, 13.8–17.1, 12	16.0, 0.98, 14.1–17.9, 26
TRW	18.6	18.2, 1.21, 15.2–19.7, 12	17.7, 0.67, 15.7–18.8, 26
PRL	5.0	5.1, 0.37, 4.4–5.7, 11	5.3, 0.42, 4.5–6.0, 26
PRW	5.7	5.0, 0.61, 3.7–6.0, 12	4.4, 0.37, 3.6–5.1, 26
M1			
MSCH	7.5	8.1, 2.32, 4.2–11.8, 23	12.5, 8.1–21.7, 12
APL	16.2	16.1, 0.60, 14.8–17.3, 24	14.9, 1.17, 13.2–17.9, 24
TRW	17.7	17.1, 1.23, 13.7–18.9, 24	17.0, 0.66, 15.8–18.2, 24
PRL	5.1	5.1, 0.43, 4.1–5.9, 24	5.2, 0.43, 4.2–5.9, 24
PRW	5.2	4.4, 0.67, 2.6–5.2, 24	4.3, 0.45, 3.6–5.6, 24

TABLE 2—(*Continued*)

	F:AM 109857	"*P.*" *leonensis*	"*M.*" *primus*
M2			
MSCH	10.1	8.7, 2.47, 3.6–11.7, 19	12.5, 8.3–20.0, 8
APL	15.2	16.1, 0.80, 14.7–17.2, 19	15.6, 1.12, 13.4–17.4, 24
TRW	16.4	16.7, 1.03, 15.4–18.4, 19	16.8, 0.71, 15.4–18.1, 24
PRL	5.0	5.0, 0.34, 4.4–5.7, 19	5.6, 0.36, 4.8–6.2, 24
PRW	4.6	4.2, 0.49, 3.3–5.0, 19	3.9, 0.38, 3.2–4.5, 24
M3			
MSCH	a12	13.1, 0.99, 11.4–14.7, 13	—
APL	13.4	15.0, 0.68, 13.7–16.1, 13	—
TRW	12.3	11.4, 1.93, 8.6–14.8, 13	—
PRL	4.1	3.9, 0.72, 2.4–4.7, 7	—
PRW	2.7	2.4, 0.43, 1.5–2.9, 7	—
Mandible			
Greatest length (l)	221	215.5, 13.8, 187–232.5, 8	216.1, 5.96, 207–225, 8
p2-p4 length (4)	46.2	46.1, 2.09, 40.3–49.5, 26	47.4, 1.94, 45.3–52.3, 11
m1-m3 length (4b)	46.8	46.7, 1.71, 42.5–49.8, 32	47.3, 1.89, 44.3–50.0, 12
p2-m3 length (5)	92.9	92.0, 3.89, 82.3–96.3, 17	94.4, 3.62, 90.5–101.1, 11
Diastema length (3)	a47	43.5, 2.79, 38.4–48.4, 21	39.2, 3.85, 33.4–47.6, 15
Symphysis length (6)	36.4	38.4, 3.25, 29.9–45.8, 23	36.6, 1.83, 32.7–40.0, 16
Symphysis width (7)	a27	26.1, 1.71, 23.2–28.5, 14	27.7, 1.63, 25.6–30.6, 12
p2 mand. depth	25.3	27.9, 1.95, 24.5–31.5, 22	26.6, 1.98, 22.8–30.2, 19
Canine length	4.7	4.2, 0.62, 3.7–5.6, 10	4.3, 0.49, 3.7–5.0, 5
Canine width	4.0	3.7, 0.83, 2.7–5.3, 9	3.7, 0.49, 3.2–4.5, 5
p2			
mcch	5.5	6.3, 0.95, 4.2–8.0, 41	—
apl	16.4	16.7, 0.87, 14.4–19.0, 41	16.6, 0.61, 15.6–17.4, 14
atw	7.5	7.6, 0.86, 5.5–9.1, 40	6.7, 0.36, 6.0–7.3, 14
ptw	8.6	8.8, 0.90, 6.9–10.5, 41	8.2, 0.47, 7.1–8.8, 14
mml	4.2	4.0, 0.58, 2.8–5.0, 41	4.7, 0.67, 3.5–5.9, 14
entl	3.0	3.8, 0.91, 2.2–5.3, 41	4.3, 1.26, 2.7–6.8, 14
p3			
mcch	6.9	7.5, 1.30, 4.7–10.7, 43	9.2, —, 8.3–10.1, 2
apl	15.2	15.5, 0.73, 13.9–17.5, 44	16.0, 0.79, 14.3–17.6, 13
atw	9.8	9.8, 0.92, 7.8–11.7, 44	9.1, 0.77, 7.8–10.2, 13
ptw	10.3	9.9, 0.80, 8.1–11.8, 43	9.3, 0.69, 8.2–10.5, 13
mml	6.7	6.9, 0.46, 6.1–7.8, 44	7.3, 0.50, 6.4–8.4, 13
entl	3.0	3.2, 1.01, 1.1–5.0, 44	3.9, 1.36, 2.1–6.6, 13
p4			
mcch	7.6	7.7, 1.29, 5.1–11.1. 41	—
apl	15.4	15.5, 0.64, 13.9–17.0, 41	16.0, 0.65, 15.0–16.9, 12
atw	10.5	10.2, 0.94, 8.3–12.1, 41	9.0, 0.70, 8.2–10.3, 12
ptw	10.0	9.7, 0.77, 8.1–11.6, 40	8.8, 0.68, 8.0–10.3, 12
mml	6.5	6.8, 0.45, 5.8–7.5, 41	7.3, 0.44, 6.6–8.4, 12
entl	3.5	3.2, 1.12, 1.5–6.2, 41	3.4, 0.83, 1.9–5.0, 12

TABLE 2—(*Continued*)

	F:AM 109857	*"P." leonensis*	*"M." primus*
m1			
mcch	7.3	6.4, 1.36, 4.2–9.1, 36	—
apl	14.7	14.8, 0.72, 13.3–16.3, 37	14.5, 0.89, 13.4–16.4, 12
atw	9.8	9.3, 1.00, 7.5–11.1, 37	8.4, 0.51, 7.5–9.4, 12
ptw	8.4	8.4, 0.90, 6.6–10.5, 37	7.4, 0.59, 6.1–8.4, 12
mml	6.5	6.6, 0.37, 5.9–7.2, 28	6.5, 0.56, 5.8–7.4, 10
entl	2.6	2.4, 1.12, 0.0–4.0, 35	1.5, 0.63, 0.8–3.0, 12
m2			
mcch	8.9	7.4, 1.41, 4.7–10.2, 33	—
apl	15.0	15.0, 0.77, 13.7–17.0, 35	15.4, 1.00, 13.9–16.7, 14
atw	8.2	8.5, 0.72, 7.1–10.0, 35	7.2, 0.52, 6.2–8.2, 14
ptw	6.9	7.6, 0.78, 6.1–9.3, 34	6.3, 0.67, 5.3–7.3, 14
mml	6.6	6.3, 0.49, 4.8–7.2, 32	6.0, 0.42, 5.3–6.9, 14
entl	3.8	3.0, 1.07, 1.0–5.2, 34	2.7, 0.84, 1.5–3.9, 14
m3			
mcch	—	10.2, 1.14, 8.6–12.3, 21	—
apl	17.2	18.2, 0.76, 16.5–20.3, 21	—
atw	6.9	6.4, 0.68, 4.8–7.3, 20	—
ptw	5.9	5.4, 0.63, 3.8–6.4, 19	—
mml	4.4	5.1, 0.52, 4.0–5.9, 20	—
entl	4.6	4.6, 0.70, 3.7–6.3, 18	—

TABLE 3

Measurements of Metacarpal III of Hemingfordian Equids

[Comparison of the metacarpal III of F:AM 109857, referred female specimen of *"Parahippus" leonensis* from the Runningwater Formation, Dawes County, Nebraska, with the sample statistics ($\bar{x}$, *s*, OR, N) of *"P." leonensis* from the Thomas Farm l.f., Gilchrist County, Florida, and *"Merychippus" primus* from the Sheep Creek Fauna, Sioux County, Nebraska. The number in parentheses refers to the same measurement used by Eisenmann (1986). All measurements in mm.]

	F:AM 109857	*"P." leonensis*	*"M." primus*
Greatest length (1)	134.9	129.7, 4.70, 122.1–141.6, 44	147.4, 5.07, 137.1–156.8, 30
Lateral length (2)	131.2	125.3, 4.36, 118.2–135.8, 44	142.6, 4.88, 132.8–151.9, 30
Mid-shaft width (3)	15.1	14.1, 1.04, 11.6–16.2, 59	13.6, 0.57, 12.2–15.0, 30
Prox. articular width (5)	18.1	18.3, 0.96, 15.6–20.9, 72	19.0, 0.77, 17.2–21.0, 30
Prox. articular breadth (6)	13.1	13.9, 0.77, 11.9–15.7, 72	14.6, 0.78, 13.0–16.3, 30
Magnum facet width (7)	17.4	16.4, 0.80, 14.1–18.7, 72	17.2, 0.61, 16.4–19.0, 30
Unciform facet width (8)	4.8	5.4, 0.61, 3.8–6.9, 72	5.4, 0.49, 4.5–6.5, 30
Max. distal width (10)	19.8	20.1, 1.29, 17.0–22.1, 58	19.1, 0.79, 17.5–21.1, 30
Distal articular width (11)	16.9	18.0, 1.10, 15.0–19.7, 58	17.6, 0.76, 16.1–19.3, 30
Max. brdth. med. condyle (14)	13.8	13.3, 0.72, 11.3–15.2, 58	13.8, 0.64, 12.2–14.9, 30

DISCUSSION: Dental characters of this species have been well described by Simpson (1930, 1932), Quinn (1955), and Forstén (1975); see also figures 7C–E, 8C–F. The known sample is principally limited to cheek-teeth, and recent efforts to collect more complete specimens have so far proven unsuccessful. Preliminary observations on the Midway sample at first appeared to contradict Simpson's (1932: 23) observation that

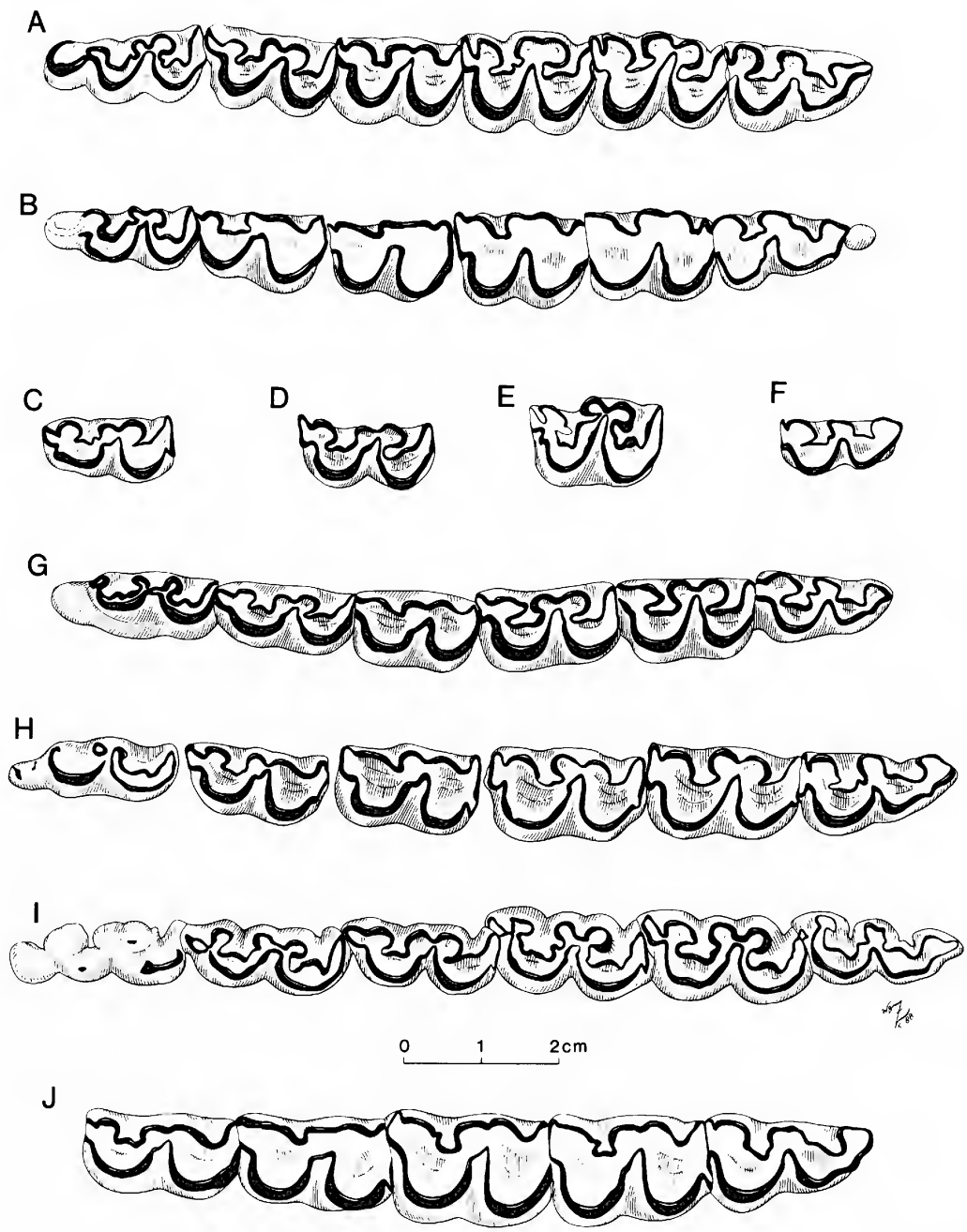

Fig. 8. Occlusal views of lower cheekteeth of Hemingfordian Equinae from Florida and Nebraska. **A.** UF/FGS V-6449, "*Parahippus*" *leonensis,* Thomas Farm, Gilchrist County, Florida. Right p2-m3. **B.** F:AM 109857, "*P.*" *leonensis,* Marshall Ranch, Dawes County, Nebraska. Left (reversed) dp1-m3. **C.** UF/FGS V-4423, "*Merychippus*" *gunteri,* Quincy Site, Gadsden County, Florida. Right m1 or m2. D–F. "*M.*" *gunteri,* Fuller's Earth Company Mine (Midway l.f.), Gadsden County, Florida. **D.** UF/FGS V-9959, right m1 or m2. **E.** UF/FGS V-9942, right p3. **F.** UF/FGS V-9937, right p2. **G.** F:AM 125597, "*M.*" *primus,* Greenside Quarry, Sheep Creek Fauna, Sioux County, Nebraska. Right p2-m3. **H.** F:AM 125576, "*M.*" *primus,* Sand Canyon Region, Box Butte Formation, Dawes County, Nebraska. Right p2-m3. **I.** F:AM 125584, "*M.*" *tertius,* Foley Quarry, Box Butte Formation, Box Butte County, Nebraska. Right p2-m3. **J.** F:AM 125593, indeterminant large merychippine, Middle of the Road Quarry, Box Butte Formation, Box Butte County, Nebraska. Left (reversed) p2-m2.

TABLE 4

Measurements of Upper and Lower Cheekteeth of "*Merychippus*" *gunteri*

[Locality abbreviations: M, Midway and Q, Quincy local faunas, both from the Torreya Formation, Gadsden County, Florida. Specimen numbers given are those of the Florida Geological Survey Collection (UF/FGS); those marked with an "*" were given to the AMNH in 1932 and are lot cataloged with the number AMNH 22683. All measurements in mm. An "a" before a measurement indicates an estimated value due to breakage or water wear.]

Spec. no.	Loc	Tooth	Side	APL	TRW	PRL	PRW	BAPL	MSCH	ROC
4979	M	DP2	R	21.7	13.7	3.8	3.7	—	6.6	—
4979	M	DP3	R	17.4	14.8	3.4	3.2	—	7.4	17
9952	M	DP34	R	17.5	14.1	3.6	3.3	15.8	6.8	—
9958	M	DP34	R	17.4	12.0	3.3	2.3	14.6	9.3	15
1432	M	P2	R	18.3	13.1	3.1	2.9	15.0	16.3	25
5040*	M	P2	R	—	12.3	—	—	—	15.1	20
4115	M	P34	R	15.0	14.0	4.2	3.5	11.8	20.1	25
5045	M	P34	L	16.0	14.7	4.2	2.9	11.9	18.4	20
4116	M	P34	R	16.2	—	—	—	12.2	13.3	—
4959	M	M2	L	16.2	18.4	6.1	4.8	—	5.7	—
5487	M	M12	L	14.8	—	3.4	2.8	10.7	—	—
5482	M	M12	L	a17	—	—	—	12.5	19.3	23
5481	M	M3	L	15.7	8.3	—	—	12.5	20.6	25
5483	M	M3	R	13.7	11.3	4.4	2.3	11.5	16.4	20
4211	M	M3	R	14.1	8.7	—	—	12.1	15.1	20
4959	M	M3	L	14.8	16.3	5.5	4.1	—	5.8	—
Spec. no.	Loc	Tooth	Side	apl	atw	ptw	mml	entl	bapl	mcch
4965	M	dp3	R	17.9	6.8	7.4	6.7	5.6	—	8.1
4965	M	dp4	R	19.0	6.5	6.4	6.6	5.5	—	9.0
5014	M	dp4	L	17.5	7.0	7.0	7.8	2.2	15.7	5.6
9940	M	dp34	R	—	7.9	—	7.2	5.3	—	7.4
4213	M	p2	L	—	5.0	6.5	2.7	5.8	13.4	14.9
4960	M	p2	L	18.2	5.5	7.3	4.7	4.5	—	11.9
1433	M	p2	R	15.0	5.8	7.4	4.5	5.0	—	9.7
9937	M	p2	R	15.5	6.5	7.4	3.4	3.9	13.6	8.7
4961*	M	p2	R	17.5	6.8	7.0	3.2	4.3	—	6.8
4960	M	p3	L	16.8	8.2	8.3	7.4	5.7	—	12.4
4964*	M	p3	L	17.0	9.1	9.1	6.8	5.8	—	12.2
4962	M	p3	L	16.7	9.4	9.3	6.6	5.1	—	9.5
4961*	M	p3	R	17.2	9.1	9.8	6.9	3.9	—	9.1
4963	M	p3	R	15.8	9.2	9.3	6.6	3.0	—	7.5
4960	M	p4	L	16.3	7.9	7.9	6.6	5.2	—	—
4964*	M	p4	L	16.6	8.7	8.9	6.5	5.1	—	—
4961*	M	p4	R	17.1	9.0	9.0	6.9	5.3	—	10.1
4962	M	p4	L	16.9	9.7	9.7	6.9	5.1	—	9.8
4963	M	p4	R	16.0	9.3	9.4	6.6	3.3	—	9.4
9954	M	p34	L	17.7	8.5	8.8	7.4	5.8	14.5	18.9
1413	M	p34	L	16.9	8.6	8.6	6.8	6.2	14.7	16.9
9961	M	p34	R	18.1	6.6	6.6	5.8	6.0	14.8	15.1
5485	M	p34	R	15.7	8.1	8.2	7.0	4.7	12.5	14.5
9942	M	p34	R	17.5	9.7	10.0	6.9	4.9	14.6	11.2
1435	M	p34	R	13.5	8.1	8.1	6.7	3.4	11.9	9.8
4117	M	m1	R	15.6	7.6	7.3	5.8	6.1	—	20.2
4960	M	m1	L	16.4	7.6	6.8	6.9	4.1	—	13.3
4962	M	m1	L	15.6	8.4	7.4	6.7	3.5	—	7.9
5014	M	m1	L	16.5	6.0	5.5	6.0	5.4	—	—
4962	M	m2	L	17.2	7.7	7.2	6.8	4.6	—	10.8

TABLE 4—(*Continued*)

Spec. no.	Loc	Tooth	Side	apl	atw	ptw	mml	entl	bapl	mcch
4423	Q	m12	R	16.7	5.7	5.4	6.2	4.5	13.2	17.3
5941*	M	m12	L	17.6	6.1	6.2	6.3	4.3	15.0	16.7
9953	M	m12	L	17.6	6.4	6.3	6.0	5.4	13.7	16.6
4423	Q	m12	L	16.4	6.1	5.8	6.2	4.3	12.3	16.0
9942	M	m12	R	16.0	6.2	6.4	5.6	4.9	13.4	12.8
3496	M	m12	R	17.0	6.3	5.3	6.0	4.9	13.1	—
5048*	M	m12	R	16.5	7.6	7.3	7.4	3.5	14.8	13.9
9959	M	m12	R	17.2	8.4	7.7	7.2	3.9	14.4	12.9
9944	M	m12	L	15.6	6.8	6.4	6.6	2.4	14.1	10.5
9945	M	m12	R	15.1	8.3	8.1	7.0	2.3	14.0	8.9
5029*	M	m12	L	14.5	9.2	8.9	—	—	14.1	6.6
9936	M	m3	R	18.4	4.9	4.2	4.7	—	20.3	18.4
5046*	M	m3	L	18.8	5.6	5.1	5.1	4.3	18.4	18.2
5055*	M	m3	L	16.0	5.2	3.9	4.6	4.3	16.7	17.0
9934	M	m3	L	17.7	5.4	4.6	5.1	3.4	17.4	16.7
9938	M	m3	L	15.8	4.6	—	—	—	18.2	16.2
9939	M	m3	L	18.7	5.6	5.1	—	—	18.7	15.7
9949	M	m3	R	18.8	5.5	4.6	4.7	—	18.0	15.4
9946	M	m3	R	18.2	5.6	5.1	4.4	5.1	18.1	13.7
9960	M	m3	R	18.1	6.3	5.7	5.3	5.1	18.2	12.2
9948	M	m3	R	18.1	5.7	5.2	4.8	3.3	17.5	14.3
9947	M	m3	R	19.2	7.4	6.6	6.3	2.8	19.2	11.5
9941	M	m3	L	18.9	7.2	6.7	5.8	3.4	19.4	9.8

". . . there is no evidence that more than one species is represented." This was based on the seemingly broad range in size and unworn crown height (table 4). The *CV*s for several parameters are high (>10), but for those elements with large sample sizes (m3s and combined m1 and m2s) measurements independent of wear (bapl) have low *CV*s. If size is excluded, the only remaining character that suggests the presence of two taxa is unworn crown height. The largest sample of unworn and slightly worn teeth at any particular locus is the m3 (N = 10). For this group, crown height measured at the metaconid averaged 15.73 mm, $s = 1.99$, $CV = 12.66$. Although this is more variation than would be expected in a single population, the distribution is not bimodal. Without larger, more complete samples, we provisionally include all Midway specimens in a single taxon, "*M.*" *gunteri.*

"*Merychippus*" *primus*
Osborn, 1918

TYPE SPECIMEN AND LOCALITY: AMNH 14187, L maxilla with P2-M2, from the latest Hemingfordian Sheep Creek Formation, Sioux County, Nebraska. Although the *exact* type locality of "*Merychippus*" *primus* is unknown, it definitely came from the highly fossiliferous complex of AMNH and subsequent F:AM sites in this region, which have yielded an extensive topotypic sample with which this species can be well characterized (Skinner et al., 1977: 343). Although originally considered a subspecific variant of *M. isonesus* by Osborn (1918), many later workers have considered this form to be a distinct, valid species, e.g., Simpson (1932), Stirton (1940), Forstén (1975), and Munthe (1979).

MATERIAL STUDIED: (1) Regardless of the exact type locality for this species, the large sample of "*Merychippus*" *primus* from Thomson Quarry in the Sheep Creek Formation is central to an understanding of the morphology of this species. The Thomson Quarry sample of "*M.*" *primus* is one of the best known for a single species of fossil horse and has been used previously in several studies to analyze paleopopulation variation and evolution (Simpson, 1944; Van Valen, 1963, 1964; MacFadden, 1989). Stratigraphically

TABLE 5

Measurements of Upper and Lower Cheekteeth of Box Butte Merychippines

[Three merychippine species are recognized in the Box Butte Formation, early late Hemingfordian, Dawes and Box Butte counties, Nebraska: "*M.*" *primus,* "*M.*" *tertius,* and a large, indeterminate species. All specimens are from the F:AM collection, and all measurements are in mm.]

Spec. no.	Tooth	Side	APL	TRW	PRL	PRW	BAPL	MSCH	ROC
				"*Merychippus*" *primus*					
125574	P2	R	21.4	14.2	3.5	3.4	—	19.2	20
125574	P3	R	18.8	16.5	4.2	3.5	—	19.6	25
125574	P4	R	17.6	16.0	4.6	3.2	—	—	—
125574	M1	R	17.2	16.7	5.1	4.1	—	—	—
125574	M2	R	16.3	13.8	4.2	2.5	—	—	30
125573	P2	R	20.6	15.6	4.1	4.1	—	17.1	20
125573	P3	R	18.7	18.0	5.0	4.4	—	17.0	25
125573	P4	R	18.1	18.1	5.0	4.2	—	18.8	25
125573	M1	R	17.1	17.6	5.6	4.2	—	15.8	25
125573	M2	R	17.0	15.9	5.5	3.6	—	—	28
125578	P2	R	20.2	15.7	3.9	3.8	17.5	17.2	23
				"*Merychippus*" *tertius*					
125579	P2	R	22.2	17.0	4.1	3.9	—	19.3	30
125579	P3	R	18.7	18.6	4.9	3.9	—	23.4	30
125579	P4	R	18.7	19.1	5.6	3.9	—	—	45
125579	M1	L	18.4	18.1	5.1	3.3	—	—	35
125579	M2	L	18.0	18.9	5.5	3.6	—	—	—
125580	P2	R	22.1	15.4	3.6	2.2	—	19.5	25
125580	P3	R	19.6	18.4	4.8	2.6	—	—	25
125580	P4	R	18.4	18.3	4.8	2.7	—	21.3	25
125580	M1	R	18.4	18.4	5.7	3.7	—	—	—
125580	M2	R	18.2	16.5	4.9	2.7	—	—	—
125589	P2	L	22.4	15.1	3.5	3.0	—	17.3	25
125589	P3	L	19.7	17.9	3.8	3.5	—	20.5	—
125589	M1	L	19.7	17.9	5.6	3.5	—	17.2	25
125587	P3	R	17.8	19.4	5.2	4.9	—	14.0	—
125587	P4	R	19.1	19.5	5.3	4.9	—	16.9	—
125587	M1	R	15.0	18.2	4.9	4.5	—	13.6	—
125587	M2	R	17.5	18.5	5.1	4.7	—	17.2	30
125591	P2	L	22.4	17.9	4.3	4.3	—	19.9	20
125591	P3	L	19.6	19.2	5.1	4.0	—	24.7	35
125591	P4	R	18.3	17.4	4.5	3.3	—	26.4	33
125591	M1	R	19.4	18.7	6.0	4.5	—	—	40
125591	M2	L	19.0	15.8	5.4	3.3	—	24.1	33
				"*Merychippus*" sp. indet.					
125592	P2	L	23.7	18.7	5.0	4.4	—	12.2	—
125592	P3	L	18.9	21.1	5.4	4.9	—	16.4	20
125592	P4	L	18.4	21.4	6.0	5.2	—	15.0	20
125592	M1	L	15.9	21.3	6.6	5.7	—	12.3	—
125592	M2	L	20.3	20.0	7.6	4.4	—	15.6	25
125596	P2	L	22.4	18.7	6.1	5.0	—	14.0	—
125596	P3	L	22.4	18.7	6.1	5.0	—	14.0	—
125596	P4	L	18.9	21.1	6.4	4.4	—	18.4	35
125596	M1	L	18.3	21.6	6.8	5.0	—	13.0	—
125596	M2	L	21.1	21.0	7.5	4.5	—	—	35
125596	M3	L	18.9	—	6.1	—	—	19.7	35

TABLE 5—(*Continued*)

Spec. no.	Tooth	Side	apl	atw	ptw	mml	entl	mcch
				"*Merychippus*" *primus*				
125577	dp2	L	20.3	8.2	9.4	7.6	1.7	4.8
125577	dp3	L	18.1	9.9	9.6	9.0	1.4	3.6
125577	dp4	L	18.4	8.4	8.0	8.7	2.1	4.8
125577	m1	L	17.4	6.6	6.2	6.7	3.9	—
125577	m2	L	18.9	5.7	5.5	6.0	6.3	—
125575	p2	L	18.3	7.3	9.2	5.1	5.8	—
125575	p3	L	18.9	9.2	9.6	7.8	5.4	—
125575	p4	L	18.7	9.0	8.5	7.6	4.9	—
125575	m1	L	16.5	8.6	7.3	6.8	2.7	—
125575	m2	L	17.5	6.9	6.0	5.9	4.1	—
				"*Merychippus*" *tertius*				
125581	p2	R	18.8	8.8	9.9	6.6	1.7	—
125581	p3	R	17.2	12.4	12.1	8.4	1.2	7.5
125581	p4	R	16.6	13.0	12.5	7.9	2.6	—
125581	m1	R	15.1	10.4	9.3	—	0.0	—
125581	m2	R	16.7	8.8	8.2	7.2	2.1	—
125581	m3	R	22.0	7.7	7.0	6.3	3.9	—
125582	p2	R	18.8	7.7	9.5	5.1	3.9	8.8
125582	p3	R	17.2	10.4	10.3	8.4	2.8	9.6
125582	p4	R	17.8	10.3	9.0	8.1	2.8	10.4
125582	m1	R	15.6	10.0	8.4	7.0	0.0	7.3
125582	m2	R	17.0	8.4	7.5	7.5	2.5	—
125582	m3	R	19.8	7.1	6.2	5.8	4.9	—
125583	p2	L	21.0	7.8	9.6	5.0	6.4	12.1
125583	p3	L	19.3	8.9	9.6	6.1	7.3	—
125583	m1	L	18.7	9.0	8.1	7.8	4.6	11.8
125588	p2	R	19.9	6.4	8.7	4.7	6.2	—
125588	p3	R	19.8	8.2	8.8	7.6	6.1	—
125588	p4	R	19.4	8.2	8.5	7.6	5.7	—
125588	m1	R	18.1	8.0	7.3	7.7	3.8	—
125590	p2	R	20.2	7.5	8.2	3.4	5.4	—
125590	p3	R	19.4	9.4	9.1	8.0	6.0	—
125590	p4	R	19.4	8.5	8.9	7.5	6.8	—
125590	m1	R	18.5	8.2	6.8	7.5	3.5	—
125590	m2	R	18.8	6.7	6.2	6.4	4.7	—
				"*Merychippus*" sp. indet.				
125594	p2	R	19.2	8.9	12.1	—	2.2	5.5
125594	p3	R	18.6	14.0	13.0	9.1	2.2	—
125594	p4	R	18.4	13.6	13.6	8.8	1.2	8.5
125594	m1	R	17.2	13.6	12.2	—	0.0	—
125594	m2	R	18.4	10.6	9.7	8.9	2.0	—

similar quarries in the Sheep Creek Formation have also produced important but not as prolific samples of "*M.*" *primus*. Principal referred specimens used in this study were AMNH 18944, 18963, F:AM 69700, 69701, 69702, 69726, and 69777 (skulls); and AMNH 21505, 21512, 24046, 90494, and F:AM 111186 (mandibles). (2) Galusha (1975) noted the presence of a merychippine very similar to "*M.*" *primus* in the Box Butte

TABLE 6

Measurements of Metatarsal III of Hemingfordian Equids

[Comparison of the metatarsal III of F:AM 125573, referred specimen of "*Merychippus*" *primus* from the Box Butte Formation, Dawes County, Nebraska, with the sample statistics ($\bar{x}$, *s*, OR, N) for *M. primus* from Thomson Quarry, Sheep Creek Formation, Sioux County, Nebraska, and for "*Parahippus*" *leonensis* from the Thomas Farm Site, Gilchrist County, Florida. The number in parentheses refers to the same measurement used by Eisenmann (1986). All measurements in mm.]

	F:AM 125573	"*P.*" *leonensis*	"*M.*" *primus*
Greatest length (1)	169.2	145.7, 6.18, 137.0–162.0, 47	163.0, 5.51, 148.8–171.1, 30
Lateral length (2)	168.4	145.1, 6.12, 136.3–161.1, 47	162.1, 5.50, 147.5–169.9, 30
Mid-shaft width (3)	14.2	14.7, 1.17, 11.6–16.7, 62	13.7, 0.96, 11.7–16.2, 30
Mid-shaft breadth (4)	14.8	13.5, 0.79, 11.8–15.1, 62	13.9, 0.67, 12.3–15.5, 30
Prox. art. width (5)	20.9	19.6, 1.00, 17.0–21.3, 88	19.1, 1.17, 17.3–22.8, 30
Prox. art. breadth (6)	17.3	14.9, 0.81, 13.9–17.0, 86	15.3, 0.90, 14.1–17.6, 30
Ectocuneiform facet width (7)	20.6	18.7, 0.85, 16.8–20.7, 87	18.4, 1.10, 16.6–22.0, 30
Cuboid facet width (8)	3.3	4.4, 0.62, 2.5–5.7, 88	4.3, 0.47, 3.4–5.5, 30
Max. distal width (10)	20.6	19.9, 1.34, 16.4–23.3, 63	19.5, 1.18, 17.0–22.8, 30
Distal art. width (11)	19.2	18.2, 1.34, 14.8–20.1, 63	17.4, 0.86, 16.0–20.4, 30
Diam. distal keel (12)	17.1	15.2, 0.84, 12.9–16.8, 62	15.2, 0.73, 13.5–17.0, 30
Min. brdth medial condyle (13)	14.4	12.7, 0.66, 11.0–14.3, 63	12.7, 0.69, 11.4–14.6, 30
Max. brdth medial condyle (14)	15.6	14.3, 0.76, 12.2–15.9, 64	14.0, 0.71, 12.4–15.8, 30

Formation (specimens listed in table 5). We agree with this observation and describe the sample in greater detail below.

DISTRIBUTION: Late Hemingfordian of Nebraska (ca. 16.5 to 17.5 Ma).

DISCUSSION: Considering the wealth of available material from the Sheep Creek Fauna of "*Merychippus*" *primus,* and its widely regarded important position in the evolutionary history of the Equidae, published morphological descriptions of this sample are surprisingly scanty. The best sources available for dental descriptions and measurements of "*M.*" *primus* are in studies of related species, such as Munthe (1979). Univariate statistics were calculated for dental, cranial, and postcranial measurements of the Sheep Creek "*M.*" *primus* sample, for comparison with those of the similar-size "*Parahippus*" *leonensis* (tables 2, 3, 5, and 6). Important quantitative differences between the two include, in "*M.*" *primus,* over 50 percent greater unworn cheektooth crown height, on average slightly longer but narrower cheekteeth also with shorter basal crown lengths, and very different limb proportions (tables 3 and 6). "*M.*" *primus* has longer, more slender distal limb bones (radius, metacarpals, and metatarsals), but shorter proximal limb elements (femur and humerus). All of the differences in limb length are significant at the $p \leq 0.001$ level. This probably reflects an ecological difference, with "*P.*" *leonensis* more adapted for forested or ecotone environments (the hypothesized paleoenvironment of Thomas Farm; Pratt, 1986, 1989; Pratt and Morgan, 1989), and "*M.*" *primus* an open-country, cursorial form.

As shown in table 1 and figure 6, "*Merychippus*" *primus* resembles "*Parahippus*" *leonensis* in a number of important cranial character states. The DPOF is very shallow with poorly defined borders and a narrow preorbital bar; there is no malar fossa or depression. The postorbital frontal region is notably domed, as in *Pseudhipparion* (Webb, 1969; Webb and Hulbert, 1986), a character used by Skinner et al. (1977) to unite the two taxa. Based on this analysis, the similarity is probably the result of parallelism. Radinsky (1984) determined that the relative skull proportions of "*M.*" *primus* had attained those of a fully hypsodont horse such as *Equus.*

The smallest of the three merychippines in the Box Butte Formation is very similar to, and probably conspecific with *"Merychippus" primus.* The teeth are slightly larger than mean values for the Sheep Creek population

(tables 2 and 5), and have slightly more complex fossette margins (figs. 7G, 8H), but both are within the observed range of the latter. The MT III of F:AM 125573 is long and slender, like those of Sheep Creek "*M.*" *primus* (table 6), and proportionally quite unlike those of "*P.*" *leonensis* and "*M.*" *gunteri.* The Box Butte and Sheep Creek samples are also similar in terms of unworn crown height, radius of curvature (20 to 30 mm), protocone shape, early protocone connection to the protoloph, and development of the metaconids and metastylids. Pending collection of larger sample sizes and more complete material, the Box Butte specimens are referred to "*M.*" *primus.*

"*Merychippus*" *tertius*
Osborn, 1918

TYPE SPECIMEN AND LOCALITY: AMNH 14180, associated palate and mandibles with nearly complete male dentition, and partial skeleton, from *Merychippus* Draw, late Hemingfordian Sheep Creek Fauna, Sheep Creek Formation, Sioux County, Nebraska (Skinner et al., 1977).

MATERIAL STUDIED: (1) From the Sheep Creek Fauna, AMNH 14180, F:AM 71365, 109959, 109964 (skulls, maxillae); AMNH 18306, 18307, 71361, 90486 (mandibles). This includes the holotypes of both "*M.*" *tertius* and "*M.*" *quintus,* which also contain associated postcranial elements. Skinner et al. (1977) and Woodburne (personal commun.) recognized three merychippine taxa in the Sheep Creek Fauna: "*M.*" *primus,* a "*M.*" *isonesus*-like species, and a *M. insignis*-like species. Only the first two of these were included in this analysis, as they are both well represented in the AMNH collections. Instead, the excellent sample from the younger Lower Snake Creek Fauna was used to determine character states for *M. insignis.* (2) From the late Hemingfordian Box Butte Formation, Dawes and Box Butte counties, Nebraska, the sample listed as "*Merychippus* cf. *M. isonesus*" by Galusha (1975: 54). Critical specimens include F:AM 125579, 125580, 125586, 125587, 125589, and 125591 (associated upper dentitions), and F:AM 125581, 125584, 125585, 125588, and 125590 (associated lower dentitions).

DISTRIBUTION: Late Hemingfordian of Nebraska (ca. 16.5 to 17.5 Ma).

DISCUSSION: Both the Sheep Creek and Box Butte formations contain, besides "*Merychippus*" *primus,* a larger (by 10 to 15%) merychippine species, "*M.*" *tertius* (table 5; figs. 7H, 8I). "*M.*" *tertius* is very similar to the well-known early to middle Barstovian "*M.*" *isonesus* (Downs, 1956, figs. 26–34; he refers to it as *M. seversus,* which is a smaller, inadequately known species). The primary differences between "*M.*" *tertius* and "*M.*" *isonesus* are the lower unworn crown height and shallower malar fossa in the former. It is likely that the two represent the endpoints of a chronocline, and they could eventually be synonymized if further study confirms this relationship. For this reason we have omitted "*M.*" *isonesus* from this study, as it did not add any phylogenetic information beyond that provided by "*M.*" *tertius.* Compared to "*M.*" *primus,* "*M.*" *tertius* is larger (table 5), has a deeper DPOF (but still relatively shallow) with a distinct but unpocketed posterior rim, and a shallow malar fossa that is poorly separated or confluent with the DPOF. Dental features distinguishing "*M.*" *tertius* from "*M.*" *primus* are longer retention of isolated protocones, stronger pli caballin on molars, relatively larger and better separated metaconid and metastylid, and a very reduced and much more frequently absent dp1.

"*Merychippus*" *carrizoensis*
Dougherty, 1940

TYPE SPECIMEN AND LOCALITY: LACM (CIT) 2552, L maxilla with M1-M3, from the late Hemingfordian Caliente Mountain region, San Luis Obispo County, California.

MATERIAL STUDIED: F:AM 110128, 110129 (skulls); 110146, 110149, and 110151 (mandibles) from the lower part of the Barstow Formation in southern California. Includes specimens from the Red Division l.f. (late Hemingfordian) and the Yermo l.f. (early Barstovian).

DISTRIBUTION: Late Hemingfordian and early Barstovian of central and southern California (ca. 15.5 to 17.5 Ma); see Quinn (1987) and Woodburne et al. (1990) for discussions on the biostratigraphy of this species.

DISCUSSION: The morphology and phylo-

genetic position of this small species has been discussed by Dougherty (1940), Downs (1956), Forstén (1975), Munthe (1979), and Quinn (1984, 1987). Buwalda and Lewis (1955) described a similar merychippine from the Kinnick Formation of the Tehachapi Mountains as a new species, "*Merychippus*" *tehachapiensis.* However, this was later considered a junior synonym of *M. carrizoensis* (Munthe, 1979). Quinn (1984) described the cranial features of "*M.*" *carrizoensis,* and recognized the presence of a well developed malar fossa as a derived equine character state. Despite its small size, great age, and plesiomorphic dental similarities with "*M.*" *primus,* "*M.*" *carrizoensis* shares both facial and dental synapomorphies with equines, and demonstrates the antiquity of this subtribe. The latter include rapidly connected protocones and relatively simple fossette margins.

Protohippus vetus Quinn, 1955

TYPE SPECIMEN AND LOCALITY: TMM 31242-71, associated maxillae containing R P3-M3 and L P2-M3, from the early Barstovian, lower Burkeville Fauna (= Point Blank Fauna of Hesse, 1943), San Jacinto County, Texas.

MATERIAL STUDIED: (1) Topotypic specimens from TMM locality 31242. (2) Additional material from other Burkeville Fauna sites in the TMM and TAMU collections, including the Summer's Ranch Sand Pit (TMM 40070) and the Burkeville l.f. of Stenzel et al. (1944). Specimens examined are listed in Table 7 or in Forstén (1975).

DISTRIBUTION: Early to middle Barstovian of the Texas Gulf Coastal Plain (ca. 13.5 to 16 Ma).

DISCUSSION: Quinn (1955) thoroughly described the dentition of the type maxilla and a single lower molar of *Protohippus vetus.* Later, Forstén (1975) referred additional topotypic material, as well as specimens from stratigraphically equivalent sites to this taxon, and provided a good account of the species' dental morphology. She placed the species in *Merychippus,* but her use of the generic name was in the traditional, broad sense. Our analysis includes only dental characters for *P. vetus,* as none of the postcranial elements listed by Forstén (1975: 27, 29) are directly associated with dentitions, and crania are unknown or presently undescribed. Replacement of *P. vetus* by the late Barstovian *P. perditus* (for which cranial and postcranial character states are known) does not change the topology of the most parsimonious cladogram to any significant degree. *Protohippus vetus* has several synapomorphies with *Protohippus* and *Calippus,* including oblique premolar protocone orientation, elongate-oval protocones, and shallow premolar ectoflexids (Hulbert, 1988a). The protocone connects in midwear, as is typical of *Protohippus.*

"*Merychippus*" *intermontanus*
Merriam 1915

TYPE SPECIMEN AND LOCALITY: UCMP 21400, associated R P2-M3, from the Barstow Fauna, upper part of the Barstow Formation, late Barstovian of the Mud Hills, Mojave County, California.

MATERIAL STUDIED: (1) There have been many subsequent topotypic specimens collected that are potentially referable to this species. These are housed principally in the F:AM, UCMP, LACM and UCR collections. (2) A sample of slightly smaller but otherwise morphologically similar specimens from the Lower Snake Creek Fauna, Olcott Formation, Sioux County, Nebraska in the F:AM collection. Primary examples are F:AM 87301 (skull) and 112336 (mandible).

DISTRIBUTION: Late Barstovian of southern California and possibly Montana (ca. 13 to 15 Ma; Dorr, 1956). Early Barstovian of Nebraska (ca. 15 to 16 Ma).

DISCUSSION: "*Merychippus*" *intermontanus* was originally described by Merriam (1915) on an associated upper dentition of uncertain stratigraphic provenience from the Barstow Formation. Subsequent stratigraphically controlled collecting has demonstrated that the species occurs only in the upper part of the Barstow section (Quinn, 1984, 1987; Woodburne et al., 1990). Additional referred material, including skulls, was described by Bernor et al. (1980), Quinn (1984), and Dorr (1956); the latter record from Montana. In a previous study (Hulbert, 1989), based on less complete material, "*M.*" *intermontanus* could not be allied to any genus or group of genera of hypsodont horses.

TABLE 7

Measurements of Upper and Lower Cheekteeth of *Protohippus vetus*

[Specimens are from the lower Burkeville Fauna, early Barstovian, San Jacinto and Washington Counties, Texas. All specimens except TAMU 2726 are in the TMM collection; all measurements are in mm. An "a" before a measurement indicates an estimated value due to breakage or water wear.]

Spec. no.	Tooth	Side	APL	TRW	PRL	PRW	BAPL	MSCH	
31242-71	P2	L	24.7	17.6	4.9	3.7	—	23.6	
31242-71	P3	L	21.2	20.8	6.5	3.5	—	30.4	
31242-71	P4	L	20.2	20.5	6.9	3.5	—	32.4	
31242-71	M1	L	19.4	19.1	6.9	3.3	—	—	
31242-71	M2	L	20.2	17.5	6.6	3.3	—	30.5	
31242-71[a]	P3	R	20.0	20.9	6.9	4.6	—	—	
31242-71[a]	P4	R	20.3	21.9	7.4	4.4	—	—	
31242-71[a]	M1	R	17.4	20.9	7.7	4.6	—	—	
31242-71[a]	M2	R	19.2	21.9	7.6	4.4	—	—	
31242-71[a]	M3	R	19.4	17.2	5.7	3.5	—	—	
31242-100	DP2	L	—	14.0	2.8	2.8	—	13.1	
31242-100	DP3	L	20.0	16.7	4.3	3.4	—	12.1	
31242-100	DP4	L	20.6	14.2	4.3	2.6	—	14.1	
31242-100[a]	M1	R	21.7	17.7	6.7	2.8	—	—	
31243-3	P34	R	19.7	22.1	7.0	4.5	17.3	15.4	
40070-3	P34	R	20.3	21.1	6.6	4.4	16.8	26.8	
40070-17	P34	R	20.9	20.4	6.0	3.4	17.1	32.2	
40070-25	M1	L	—	a18	6.5	3.3	13.8	30.1	
Spec. no.	Tooth	Side	apl	atw	ptw	mml	entl	bapl	mcch
31242-84	dp2	R	22.1	7.3	10.1	7.5	5.2	—	5.9
31242-84	dp3	R	20.2	8.8	9.5	9.6	3.5	—	—
31242-84	dp4	R	22.7	8.8	8.1	9.5	4.6	19.9	10.5
31242-82[b]	m1	R	20.3	8.2	7.5	7.3	—	—	—
TAMU 2726	p34	L	18.4	9.2	8.8	8.0	6.6	15.9	22.3
31242-102	m12	L	19.5	7.8	6.9	7.4	5.0	15.2	26.3

[a] Measured on sectioned surface.

[b] Measured 10 mm below unworn occlusal surface.

"*Merychippus*" *coloradense* (Osborn), 1918

TYPE SPECIMEN AND LOCALITY: AMNH 9094, two isolated upper molars, probably associated M1 and M2, and associated postcranial elements, from the late Barstovian Sand Canyon Fauna, Ogallala Group, Logan County, Colorado.

MATERIAL STUDIED: Of the material referred to this taxon by MacFadden (1984a), the majority of character states were taken from two partial skeletons, F:AM 69506 from the Sand Canyon Fauna, and F:AM 69511, Boulder Quarry, Lower Snake Creek Fauna, Olcott Formation, Sioux County, Nebraska. F:AM 69500 and 69503, two skulls from New Mexico (MacFadden, 1984a), provided additional information.

DISTRIBUTION: Early Barstovian to early Clarendonian of Nebraska, Colorado, and New Mexico (ca. 11 to 16 Ma).

DISCUSSION: This taxon was recently revised as *Neohipparion coloradense* by MacFadden (1984a), who provided descriptions and illustrations of the crania and dentition. Webb and Hulbert (1986) and Hulbert (1987, 1988c, 1989) concluded that "*N.*" *coloradense* was the sister taxon to both *Pseudhipparion* and *Neohipparion*; thus its inclusion in *Neohipparion* makes that genus paraphyletic. Salient characters include large size ($\bar{x}$ UTRL = 127 mm), a moderately deep DPOF with a well-developed posterior rim and a slight pocket, narrow preorbital bar, protocones isolated until middle wear stages with large spurs, shallow premolar ectoflex-

ids, well-developed protostylids, and large metastylids equal in size to the metaconids.

Merychippus insignis Leidy, 1874

TYPE SPECIMEN AND LOCALITY: ANSP 11276, a fragmentary right maxilla with DP2-3, collected from the Bijou Hills, South Dakota. Locality data uncertain but probably from the Barstovian Fort Randall Formation (Skinner and Taylor, 1967).

MATERIAL STUDIED: (1) Available topotypic material from the Bijou Hills in the F:AM collection, especially F:AM 87011. (2) The sample referred to *M. insignis* by Skinner and Taylor (1967) from Echo Quarry, Sioux County, Nebraska, especially F:AM 87002, 87003, 87005, and 87045 (skulls), and 87072, 87078, 87077, and 87085 (mandibles). (3) Specimens from New Surface, Humbug, and East Sand quarries from the Olcott Formation of Sioux County including AMNH 18297, 18299 (skulls) and F:AM 111681, 111688 (mandibles).

DISTRIBUTION: Early Barstovian of Nebraska and South Dakota (ca. 15 to 16 Ma). Possibly also the middle Barstovian of Nebraska, the early to middle Barstovian of Texas and Colorado, and the early Barstovian of California.

DISCUSSION: Skinner and Taylor (1967) provided complete descriptions of the skull and upper dentition of this taxon. Their referral of the Lower Snake Creek sample to *Merychippus insignis* was recently rejected by Evander (1986). We discuss this question at length below and, contrary to Evander, conclude that the type material of *M. insignis* does fall within the range of variation observed in the Lower Snake Creek population for systematically important characters. The species (and genus) may yet be categorized as a nomen dubium, however, if future work demonstrates that the type specimen is not specifically diagnostic. Whatever its final designation, the Sioux County population represents a well-sampled, phylogenetically important taxon, and it is the primary source of morphological information for this taxon in the present study. Skinner and Taylor (1967) also referred unspecified material from the Pawnee Creek Formation, Colorado, and the Trinity River Pit 1, Texas Gulf Coastal Plain, to *M. insignis*. These specimens were not examined in the course of this study, but are provisionally included in our discussions of merychippine biogeography. *Merychippus insignis,* or a closely related form, has also been recognized in the older Sheep Creek Fauna of Nebraska (see discussion above under "*M.*" *tertius*), and in the Green Hills Fauna (early Barstovian) of California (Woodburne et al., 1990). Voorhies (1990) presented a preliminary description of a relatively young sample of *M. insignis* from the Norden Bridge Quarry, early late Barstovian of Nebraska.

"*Merychippus*" *goorisi*
(MacFadden and Skinner), 1981

TYPE SPECIMEN AND LOCALITY: F:AM 73940, skull with R and L C, P2-M3, from the early Barstovian Trinity River Pit 1, Burkeville Fauna, San Jacinto County, Texas.

MATERIAL STUDIED: (1) The topotypic sample (listed in MacFadden and Skinner, 1981; as modified by Woodburne, personal commun.), which includes several skulls (F:AM 73900, 73942, 73943, 78952), numerous maxillae, and several mandibles (F:AM 69556, 113058, 113064). However, no postcranial elements are directly associated with cranial material, preventing unequivocal identification. Note that MacFadden's (1984a) referral of TMM 31242-71 to this species was an error, as that specimen is the type of *Protohippus vetus.* (2) Previously undescribed material in the UF collection from the Sweetwater Branch Site, Arcadia Formation, Polk County, Florida, as listed in table 8.

DISTRIBUTION: Early Barstovian of the Gulf Coastal Plain of Texas and Florida (ca. 14.5 to 16 Ma).

DISCUSSION: This dentally primitive hipparionine was described in a recent series of papers (MacFadden and Skinner, 1977, 1981, 1982; Skinner and MacFadden, 1977; MacFadden, 1984a). These authors concluded that the species was the sister taxon to a particular clade of advanced hipparionines, *Cormohipparion,* based on its facial characters. It was referred to this genus despite its merychippine-grade cheekteeth (Forstén, 1982; MacFadden and Skinner, 1982). Hul-

TABLE 8

Measurements of Upper and Lower Cheekteeth of "*Merychippus*" *goorisi* from Florida

[Specimens are from the Sweetwater Branch Site, Phosphoria Mine, Arcadia Formation, early Barstovian, Polk County. All measurements are in mm. An "a" before a measurement indicates an estimated value due to breakage or water wear.]

Spec. no.	Tooth	Side	APL	TRW	PRL	PRW	BAPL	MSCH	ROC
UF 93341	DP34	R	—	13.4	2.6	2.2	—	9.6	—
UF 93293	DP34	R	19.8	16.5	4.5	3.9	17.6	6.3	—
UF 93342	P34	R	21.8	20.9	5.6	3.9	18.6	26.3	33
UF 93297[a]	P34	R	20.7	21.1	6.0	4.3	—	a25	34
UF 93294	P34	L	20.0	21.2	6.3	4.2	17.9	a24	—
UF 93343	P34	R	21.1	20.9	5.5	4.3	17.8	a21	—
UF 93298	P34	R	21.8	a22	—	—	17.7	—	—
UF 93295[a]	M3	L	20.7	17.8	5.5	4.0	18.1	24.2	30
UF 93296[a]	M3	R	19.9	20.5	6.3	4.5	16.4	22.0	28
Spec. no.	Tooth	Side	apl	atw	ptw	mml	entl	bapl	mcch
UF 93339	dp3	L	20.6	6.9	6.7	6.9	6.6	19.7	11.3
UF 93291	p34	L	18.1	11.9	12.1	—	2.5	—	a8
UF 93338	m1	R	20.9	10.0	8.8	9.4	4.6	17.6	21.7
UF 93292[a]	m3	L	26.8	9.3	8.3	7.9	3.6	28.3	13.9

[a] Measured on sectioned surface.

bert (1988c), using material not studied by MacFadden and Skinner, hypothesized that "*M.*" *goorisi* was the sister taxon not only to *Cormohipparion,* but to *Nannippus* as well. The three share very deep, well pocketed DPOFs with distinct anterior margins; protocone isolated until late wear stages; hypoconal groove open to base of crown; and well-developed protostylids. *Nannippus* and *Cormohipparion* share (exclusive of "*M.*" *goorisi*) a long preorbital bar, thickly cemented deciduous premolars, elongate-oval protocones, reduced protoconal spurs, shallow premolar ectoflexids, plicated isthmuses, and increased unworn crown height (Hulbert, 1988c). Therefore, while "*M.*" *goorisi* is excluded from *Cormohipparion,* its relative phylogenetic position from that originally proposed by MacFadden and Skinner (1981) is retained; the only change is the insertion of *Nannippus.*

In 1985, R. Carter and J. Pendergraft discovered one of the oldest-known faunas from the Hawthorn Group in south-central Florida. Previously the oldest fauna from the Bone Valley Region was late Barstovian (the Bradley Fauna of Webb and Hulbert, 1986), and broadly comparable with the Cold Spring Fauna of Texas and faunas derived from the Valentine Formation of Nebraska. The new locality, the Sweetwater Branch Site in the Phosphoria Mine, contains three species of equids, a rhinocerotid (cf. *Peraceras hessei*), several poorly represented artiodactyls including a camelid and a dromomerycid (cf. *Bouromeryx* sp. from Trinity River Pit 1), a very small mustelid, *Alligator,* snakes, and emydid turtles. The entire assemblage is presently under study by Hulbert and Webb. The fossils were recovered from a clay lens immediately overlying indurated dolostone of the Arcadia Formation, that represents Unit 1 of Webb and Crissinger (1983). The equids, rhinocerotid, and dromomerycid in particular suggest a Barstovian age, and the horses are much more primitive than those of the late Barstovian Bradley Fauna (Webb and Hulbert, 1986; Hulbert, 1988a, 1988c). They are more similar instead to taxa from early Barstovian faunas (e.g., Lower Snake Creek, Burkeville). Another indication of a pre-late Barstovian age is the complete lack of proboscidean material.

The Sweetwater Branch equids are represented by three taxa, "*Merychippus*" *goorisi, Merychippus* sp. cf. *M. brevidontus,* and a parahippine. The latter, known from just three teeth (UF 93300, 93336, 93337), is shorter

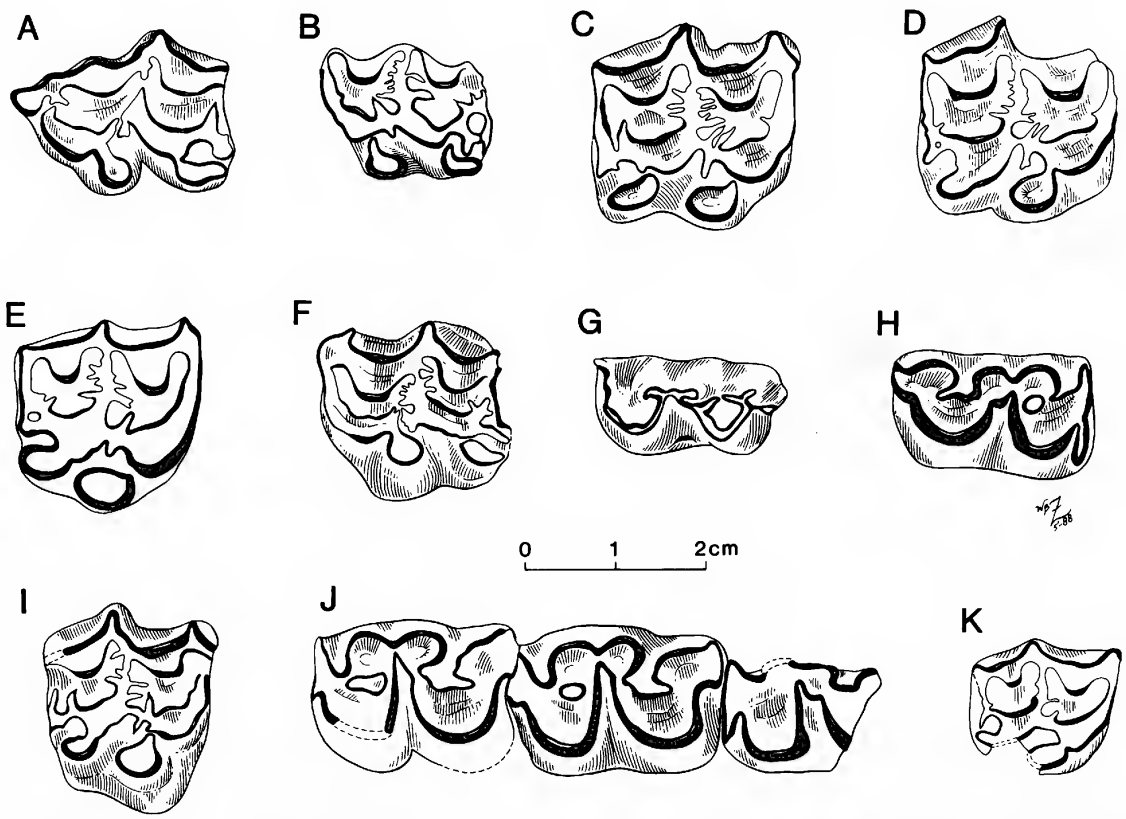

Fig. 9. Occlusal views of upper and lower cheekteeth of early Barstovian merychippines from Florida. A, B. "*Merychippus*" sp., cf. "*M.*" *isonesus,* Nichols Mine, Arcadia Formation, Polk County. **A.** UF 107056, left P2. **B.** UF 107057, left M1 (?). C–H. "*M.*" *goorisi,* Sweetwater Branch Site, Phosphoria Mine, Arcadia Formation, Polk County. **C.** UF 93342, right P3 or P4. **D.** UF 93343, right P3 or P4. **E.** UF 93296, right M3 (sectioned surface). **F.** UF 93293, left DP3 or DP4. **G.** UF 93339, left dp3. **H.** UF 93338, right m1 or m2. **I.** UF 93287, *Merychippus* sp., cf. *M. brevidontus,* Sweetwater Branch Site, Phosphoria Mine, Arcadia Formation, Polk County. Right P4. **J.** UF 65551, "*Merychippus*" sp., cf. "*M.*" *isonesus,* Smith Mine, Torreya Formation, Gadsden County. Associated left p3-m1. **K.** UF 65560, "*Merychippus*" sp., near "*M.*" *primus,* La Camelia Mine, Torreya Formation, Gadsden County. Right M3.

crowned than "*Parahippus*" *leonensis,* with broader, more poorly cemented teeth, and smoother, uncrenulated enamel. The crochet is large and the lingual cingulum is absent on the upper premolar; the lowers lack a labial cingulum. *Merychippus* cf. *brevidontus* is represented by two whole teeth and possibly some fragments (fig. 9I). They resemble described uppers of *M. brevidontus* from California and Oregon (Bode, 1934; Scharf, 1934) in their complex enamel plications; oval, disconnected protocones with strong spurs; and very short crown heights, but are about 15% smaller than the type material of *M. brevidontus.* UF 93287, a slightly worn P3 or P4, has a MSCH of only 18.0 mm, and UF 93289, a slightly worn M3, a MSCH of 16.1 mm. Unworn values would have been 2 to 5 mm greater, thus falling within the range of *M. brevidontus* given by Bode (1934). The most common equid from the Sweetwater Branch Site (15 teeth) falls within the range of variation of "*M.*" *goorisi* from Trinity River Pit 1 in unworn crown height, occlusal surface dimensions, enamel complexity, and tooth curvature (fig. 9C–H; table 8). The higher crowned (up to 35 mm in P3-M2), more heavily cemented cheekteeth, strong protostylids, and very complex fossette plications distinguish this sample from *M. insignis.* This

represents the first record of "*M.*" *goorisi* outside southeastern Texas.

"*Merychippus*" sp. near "*Merychippus*" *sejunctus*

MATERIAL STUDIED: The sample for this taxon comes from the Frick Trinity River Pit 1 locality, San Jacinto County, Texas and is of early Barstovian age. In Tedford et al. (1988), this sample was listed as "*Merychippus*" *sejunctus*. It includes several skulls (F:AM 69551, 69554, 69556) and mandibles (F:AM 112554, 112557, 112559), but no postcranial elements can be unequivocally assigned to this taxon.

DISTRIBUTION: Early Barstovian of Texas Gulf Coastal Plain (ca. 14.5 to 15 Ma).

DISCUSSION: This sample bears the same relationship with "*Merychippus*" *sejunctus* as "*M.*" *tertius* does with "*M.*" *isonesus*; i.e., it forms the older portion of a morphocline. Both of these lineages present interesting combinations of character states, some that have traditionally been associated with hipparionines, and others with equines (Hulbert, 1989). The most important of the latter is a shallow malar fossa. The Trinity River sample also exhibits relatively rapidly connected protocones. Its hipparionine features include well-developed pli caballins, moderately complex fossette margins, and well-separated metaconids and metastylids.

Pliohippus mirabilis (Leidy), 1858

TYPE SPECIMEN AND LOCALITY: USNM 569, R maxillary fragment with DP3, DP4, and M1, from the Niobrara River region, north-central Nebraska. The exact formation and age are unknown, but judging by referred material it was probably from the Valentine Formation.

MATERIAL STUDIED: (1) A large sample of skulls, maxillae, mandibles (some associated with skulls), and a few skeletons from the late Barstovian Devil's Gulch Horse Quarry, Devil's Gulch Member, Valentine Formation, Brown County, Nebraska (Skinner and Johnson, 1984). Relatively complete specimens include F:AM 60801, 60804, 60810, 60811, 60823, and 60824. (2) A referred sample from the early late Barstovian Pawnee Creek Formation, including the Frick Horse and Mastodon Quarries (Tedford et al., 1988) and earlier-collected AMNH material such as the holotype of "*Merychippus*" *campestris* Gidley (AMNH 9069).

DISTRIBUTION: Middle to late Barstovian of Nebraska and Colorado (ca. 12 to 15 Ma); late Barstovian of Florida (Hulbert, 1988c, table 10).

DISCUSSION: A distinctive deep malar fossa has been known to characterize *Pliohippus mirabilis* since Leidy's (1858) original description. Gidley (1907) recognized that this and other characters united it with Clarendonian *Pliohippus*, a referral followed by Osborn (1918). Stirton (1940) ignored this evidence, and suggested synonymy with the similar-aged *Protohippus perditus*, a taxon without a malar fossa. Hulbert (1988a) outlined the cranial and dental differences between *Protohippus* and *Pliohippus*, and in effect resurrected Gidley's definitions of these two clades.

Pliohippus mirabilis also has a deep, pocketed DPOF located well anterior to the orbit (mean preorbital bar length = 18.7 mm). Its relatively high-crowned cheekteeth (unworn M1 MSCH ca. 52 mm) have simple fossette margins, very rapidly connected protocones, and very weak protostylids. Its lower deciduous premolars lack ectostylids, a synapomorphy uniting *Pliohippus* with *Astrohippus* and *Equus* (Hulbert, 1989). The lateral toes of *P. mirabilis* retain three phalanges, but they are notably reduced relative to those of its protohippine and hipparionine contemporaries, and most likely nonfunctional.

Hipparion shirleyae MacFadden, 1984

TYPE SPECIMEN AND LOCALITY: F:AM 73950, skull, mandible, and nearly complete postcranial skeleton, from the late Barstovian Wright Farm Site, Cold Spring Fauna, Polk County, Texas.

MATERIAL STUDIED: (1) Topotypic hypodigm as published in MacFadden (1984a), especially F:AM 73950 and 99384. (2) Material from other sites in the Cold Spring Fauna, including McMurry Pits 1 and 2 (F:AM), J. Donahoe Farm Site (TMM locality 31219), Polk County Sites 2 and 3 (TMM 31183 and 31200), and the Noble Farm Site (TAMU).

Includes F:AM 73951 and 99386 (skulls), and F:AM 99385, 99389, and 99390 (mandibles).

DISTRIBUTION: Late Barstovian of the Texas Gulf Coastal Plain (ca. 12 to 13.5 Ma).

DISCUSSION: The ending of the species name is here corrected to conform with the gender of the person after whom the taxon was named (Shirley Skinner). Such a change is required by Article 32 of the International Code of Zoological Nomenclature (Ride et al., 1985). MacFadden (1984a) presented a description of the relevant characters of this small (UTRL $\bar{x} = 102$ mm, N = 4) hipparionine. Character states were taken primarily from the relatively complete topotypic sample. The species has a deep nasal notch, a relatively long preorbital bar, long symphysis, and an absent metastyle, all synapomorphies with other North American species of *Hipparion* (Hulbert, 1988c).

ANALYTICAL METHODS

Cladograms for the taxa and characters described above were generated on an 80286/80287-based microcomputer by the PAUP (Phylogenetic Analysis Using Parsimony) program version 2.4.1 developed by David Swofford. Platnick (1987) provided a useful review and comparison of PAUP and similar programs. "*Parahippus*" *leonensis* was used as an outgroup to determine character state polarities in all runs. Characters with the same state in all 13 taxa, or that had only one derived state among the 12 ingroup taxa were deleted from the computational part of the analysis. This left 39 characters with which to assess relationships, and 7.1% of the character states had to be coded as missing. The branch-and-bound option of PAUP was used to generate the most parsimonious cladogram for the 13 taxa (Swofford, 1985; Platnick, 1987), although equivalent results were obtained with the faster SWAP = GLOBAL and MULPARS options.

Characters with more than two possible states were treated as ordered characters. Parsimony, or minimizing parallelism and evolutionary reversals, is a widely used criterion for selecting the "best" cladogram among the thousands of possible solutions (Sober, 1983). Analyses were run both with equally weighted characters (the default option), and with the WEIGHTS SCALE option that scales the observed character states between the interval 0 and 1 based on the number of possible states per character. The purpose of the latter option is to avoid unduly weighting multistate characters relative to binary characters, especially those that are arbitrarily subdivided on quantitative criteria (Swofford, 1985; Goldman, 1988). Since many of our characters are of this type, results using this option were given precedence a priori over those produced using equally weighted characters. Using the BBSAVE option, hundreds of cladograms were generated that were less than 5 percent longer than that of minimum length. As there is of course no guarantee that the evolution of these horses proceeded in a strictly parsimonious manner, some of the more interesting of these slightly less parsimonious cladograms are also discussed below.

RESULTS

Cladistic analysis was performed on the character matrix (table 1) using the methods described above. With the WEIGHTS SCALE option in effect, PAUP analysis produced a single most parsimonious cladogram (fig. 10) that has a length of 64.85 steps and a consistency index of 0.61. There were many other arrangements of the 12 ingroup taxa that were only slightly less parsimonious. Analysis with equally weighted characters produced two equally parsimonious arrangements, each with lengths of 128 steps. One is identical to that produced with scaled characters (fig. 10). The other differs only in the position of the protohippine species ("*M.*" *intermontanus* and *P. vetus*), that are moved to form the sister group of the hipparionines (fig. 11B). Under the WEIGHTS SCALE option this arrangement is 0.58 steps longer than that shown in figure 10, and is less parsimonious than three additional arrangements. As there are well over 100 possible arrangements slightly longer than the most parsimonious one (figs. 11, 12), we are disinclined to suggest that the cladogram in figure 10 must represent the true evolutionary history of the group. It is merely the most likely candidate among many possibilities. Future in-

vestigations are likely to amend the data in three ways: (1) addition of currently undescribed, undiscovered, or poorly known taxa (the reasons for including or excluding taxa were discussed above); (2) addition of more characters; and (3) improving the character matrix with discoveries of currently unknown character states and correcting any misinterpretations. For these reasons we prefer to dwell on the similarities observed among the most and "almost"-most parsimonious cladograms (and their implications).

Four nodes (1, 2, 3 and 7 in fig. 10) are shared among all 250 cladograms with least length. Nodes 6 and 11 are also strongly supported and found in most of these arrangements. "*Merychippus*" *gunteri* and "*M.*" *primus* are hypothesized to form the successive sister groups to the remainder of the merychippines plus the hypsodont genera. This arrangement differs from that of Stirton (1940; fig. 4), in which "*M.*" *primus* was regarded as the most primitive species of the subgenus *Protohippus* (and thus broadly ancestral to *Calippus, Pliohippus,* and *Equus*), and "*M.*" *gunteri* was the most primitive species of the subgenus *Merychippus* (and thus ancestral to the hipparionines). In Stirton's phylogeny, as in Quinn's (fig. 5), the closest common ancestor of hipparionines and equines was of parahippine grade. However, nodes 1, 2, and 3 in figure 10 are each supported by numerous synapomorphies, which tends to falsify the hypotheses of Stirton and Quinn, and suggests instead that the hypothetical closest common ancestor of the hipparionines and equines was of merychippine grade (node 3). Seven derived character states are shared by "*M.*" *gunteri* and all other merychippines at node 1, including more cement on the cheekteeth (characters 20 and 21), better developed pli caballins (30 and 31), a strong pli entoflexid (57), shallower p2 ectoflexid (62), and increased crown height (71). This assumes that the character states for these traits are primitive in "*Parahippus*" *leonensis* relative to its common ancestor with merychippines. A general survey of parahippines validates this assumption, but it needs to be confirmed with a detailed phylogenetic analysis. No known character states of "*M.*" *gunteri* are uniquely derived relative to "*P.*" *leonensis* and other merychippines (at node 12); however the species is still inadequately known.

At node 2 of figure 10, "*Merychippus*" *primus* and other merychippines (excluding "*M.*" *gunteri*) are united by 10 synapomorphies, including a more oval protocone (23), earlier protocone connection (27 and 18), earlier hypoconal groove closure (38 and 39), reduction of the dp1 (45), and better separated metaconid and metastylid (55 and 56). The facial morphology of "*M.*" *primus* (fig. 6C) retains the primitive states observed in "*P.*" *leonensis,* the most important of which is a very shallow DPOF. Earlier studies (e.g., MacFadden, 1984a; Webb and Hulbert, 1986; Hulbert, 1987) often assumed that a deep DPOF was primitive for advanced equids—as that state is found in *Miohippus,* anchitheriines, *Archaeohippus,* and some species of *Parahippus* s.l.—and assumed that the shallow to moderate fossa in taxa such as *Neohipparion, Pseudhipparion, Protohippus* and *Calippus* was derived. The use of "*P.*" *leonensis* and "*M.*" *primus* as outgroups for this character suggests the reverse, that the very deep DPOF found in *Pliohippus* and *Cormohipparion* were independently derived. At node 13, there are four autapomorphies for "*M.*" *primus*: very early protocone connection (27 and 28); reduced DP1; and very gracile metapodials. These diminish the likelihood that "*M.*" *primus* was directly ancestral to any younger clade of horses.

At node 3 (fig. 10), the 10 merychippine species exclusive of "*Merychippus*" *gunteri* and "*M.*" *primus* are united by 7 synapomorphies: a moderately deep DPOF with a distinct posterior rim (3 and 5), thickly cemented permanent cheekteeth (21), absence of the dp1 in adults (45), expanded metaconid and metastylid (54), increased size (70), and unworn crown height (71). There are several equally parsimonious pathways for the evolution of increased crown height when the taxa are arranged as in figure 10. The sequence of steps shown in figure 10 minimizes reversals and maximizes parallel increases in crown height. Even so, one occurrence of decreasing crown height (at node 17) is necessary to achieve overall parsimony. Unless accompanied by a decrease in size (so that relative crown height or hypsodonty remains constant or increases), decreases in crown

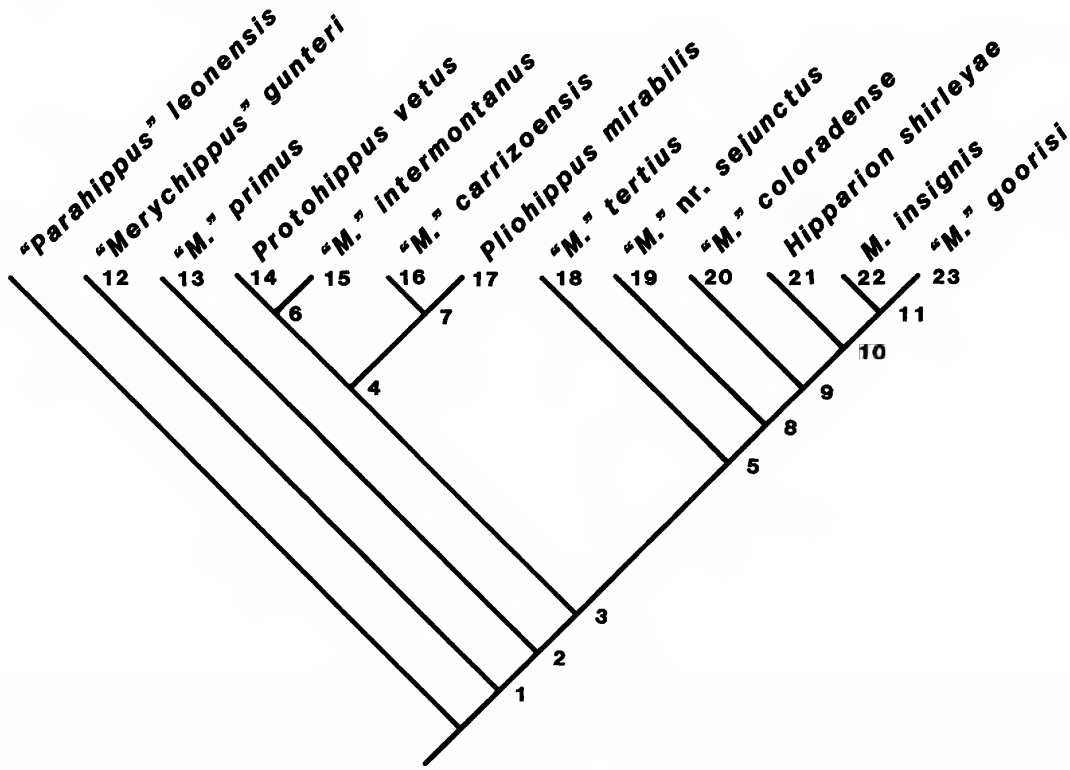

Fig. 10. PAUP-derived cladogram expressing the most parsimonious phylogenetic relationships among the 12 ingroup taxa based on the distribution of character states in table 1. "*Parahippus*" *leonensis* was used as an outgroup in the analysis. This arrangement requires 64.85 steps using the WEIGHTS SCALE option, and 128 steps with equally weighted characters. It has a consistency index of 0.61 in either case. This cladogram is supported by the following list of synapomorphies. Also listed are unique autapomorphic character states of terminal nodes, even though these were not included in the PAUP analysis. Numbers refer to codes for characters and character states defined in the text on pp. 15–19. Within the parentheses, the code number for the character is listed to the left of the colon and the hypothesized derived state to the right of the colon. **Node 1:** thin and patchy layer of cement on deciduous premolars (20:1); moderately thick layer of cement on permanent cheekteeth (21:1); pli caballin single, well developed, persistent on premolars (30:2); small, nonpersistent pli caballin on molars (31:1); pli entoflexid (57:1); moderately deep p2 ectoflexid (62:1); unworn M12 MSCH 23–28 mm (71:1). **Node 2:** oval protocone (23:1); protocone-protoloph connection forms during early moderate wear stage on P34 (27:3) and during early wear stage on M12 (28:2); M12 protocone connects to hypocone in late wear stage (29:1); internal fossette plications simple and nonpersistent (33:2); hypoconal groove closed in moderate wear stage on P34 (38:2) and M12 (39:2); dp1 reduced or rudimentary (45:1); metaconid-metastylid well separated in early wear stage (55:1); distinct metaconid and metastylid on p2 (56:1). **Node 3:** frontal bones not domed (2:1); DPOF depth shallow (3:2); DPOF with distinct posterior rim (5:1); very thick layer of cement on permanent cheekteeth (21:2); dp1 vestigial or absent (45:2); expanded metaconid and metastylid (54:1); UTRL between 105 and 125 mm in moderate wear stage (70:2); unworn M12 MSCH 28–33 mm (71:2). **Node 4** (Equini): DPOF depth moderate (5:2); protocone-protoloph connection during early wear stage (27:2); hypoconal lake on P34 (40:1); small, labial p34 metaconid (66:1); small, lingual m12 metastylid (67:1). **Node 5** (Hipparionini s.l.): well developed and persistent pli caballin on molars (31:2); MC V articulates primarily with MC IV (79:1). **Node 6** (Protohippina): moderate preorbital bar length (7:1); elongate-oval protocone (23:2); ROC upper cheekteeth 40–70 mm (43:1); well developed protostylids on dp34 (48:2), moderately developed on p3-m3 (52:1); unworn M12 MSCH 33–38 mm (71:3). **Node 7** (Equina): deep posterior pocket on DPOF (5:3); deep malar fossa (12:2); protocone-protoloph connection very early wear stage on both P34 (27:0) and M12 (28:0); reduced pli caballin on P34 (30:1); very simple internal fossette plications (33:1). **Node 8:** persistent internal fossette plications (33:3); moderate protostylids on dp34 (48:1) and p3-m3 (52:1); persistently separated metaconid and

height are relatively unlikely in herbivore evolution. Probably there was even more parallelism for increased crown height than is indicated in figure 10. Removal of character 71 (unworn crown height) from the analysis does not affect the most parsimonious arrangement of the 12 taxa.

The 10 taxa united at node 3 of figure 10 can be arranged in many ways without greatly increasing the length of the cladogram (fig. 12). The taxa can be subdivided into four groups, equines ("*M.*" *carrizoensis* and *Pliohippus mirabilis*), protohippines ("*M.*" *intermontanus* and *P. vetus*), hipparionines ("*M.*" *coloradense,* "*H.*" *shirleyae, M. insignis,* and "*M.*" *goorisi*), and "*M.*" *tertius* plus "*Merychippus*" sp. cf. "*M.*" *sejunctus.* The positions of the latter two species are the most labile in the analysis, as suggested by figure 11. If those two are ignored, the analysis supports both the hypothesis that hipparionines are the sister group of equines plus protohippines (figs. 10, 11A), and the hypothesis that equines are the sister group of hipparionines and protohippines (fig. 11B, C). A close relationship between equines and hipparionines, similar to that suggested by Quinn (1955), is not as strongly supported (such an arrangement would require at least two additional steps). The hypothesis that equines and protohippines are closest sister taxa (i.e., fig. 10) is preferred for two reasons. First, it is more parsimonious when the character weights are scaled, a methodology favored when many multistate characters are being analyzed (Swofford, 1985). Second, the synapomorphies uniting equines and protohippines on average are subject to less parallelism than those uniting hipparionines and protohippines. Putative hipparionine-protohippine synapomorphies include a longer preorbital bar, increased unworn crown height, and stronger protostylids. The possibility of a hipparionine plus protohippine clade de-

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metastylid (55:2); unworn M12 MSCH 33–38 mm (71:3). **Node 9** (Hipparionini s.s.): protocone-protoloph connection during late moderate wear stage on the P34 (27:4) and M12 (28:4); well-developed metastyle (35:2); M12 hypoconal groove closed in late wear stage (39:1); hypoconal lake on P34 (40:1). **Node 10:** DPOF with distinct ventral rim (6:1); moderate preorbital bar length (7:1); moderately complex fossette plications (33:4); P34 hypoconal groove closed in late wear stage (38:1). **Node 11:** multiple pli caballin on premolars (30:3); persistent external fossette plications (32:1); well-developed protostylids on dp34 (48:2). **Node 12:** no known apomorphic character states. **Node 13:** reduced DP1 size; protocone-protoloph connection in early wear stage on P34 (27:2) and very early wear stage of M12 (28:1); slender, elongated metapodials. **Node 14:** oblique protocone orientation on P34; loss of hypoconal lake on P34 (40:0); reduced depth of ectoflexid on p34 (63:1). **Node 15:** thick coating of cement on deciduous premolars (20:2); hypoconal lake present on molars (41:1). **Node 16:** DPOF with distinct ventral rim (6:1); moderate preorbital bar length (7:1); thick coating of cement on deciduous premolars (20:2); early connection of protocone and hypocone (29:2); hypoconal groove closed in early wear stage on premolars and molars (38:3, 39:3); hypoconal lake present on molars (41:1); reduced P34 parastyle; reduced or absent ectostylids on deciduous premolars; reduced depth of ectoflexid on p34 (63:1); UTRL between 125 and 140 mm (70:3); unworn M12 MSCH 48–55 mm (71:6). **Node 17:** oval DPOF (8:1); relatively elongated muzzle (16:3); moderate layer of cement on permanent cheekteeth (21:1); dp1 small but persistent (45:1); metaconid-metastylid subequal in size (66:0); UTRL between 90 and 105 mm (70:1); unworn M12 MSCH 23–28 mm (71:1). **Node 18:** oval DPOF (8:1); shallow malar fossa (12:1); malar fossa and DPOF confluent; decreased muzzle length (16:1). **Node 19:** shallow malar fossa (12:1); protocone-protoloph connection in early wear stage on P34 (27:1); unworn M12 MSCH 38–43 mm (71:4). **Node 20:** DPOF with shallow posterior pocket (5:2); elongate-oval protocone (23:2); ROC of upper cheekteeth 40–70 mm (43:1); shallower premolar ectoflexids (62:2, 63:1); UTRL between 125 and 140 mm (70:3); unworn M12 MSCH 38–43 mm (71:4). **Node 21:** deep nasal notch; very long preorbital bar (7:2); elongate-oval protocone (23:2); metastyle absent or very weak (35:0); UTRL between 90 and 105 mm (70:1). **Node 22:** loss of ventral rim of DPOF (6:0); hypoconal lake on molars (41:1). **Node 23:** deep DPOF (3:3) with large posterior pocket (5:3) and distinct anterior rim; reduced lacrimal bone that is not involved with DPOF; protocone-protoloph connection not until very late wear stage (27:5, 28:5); complex internal fossette plications (33:5); persistently open hypoconal grooves (38:0, 39:0) that do not form lakes (40:0); well developed protostylids on p3-m3 (52:2).

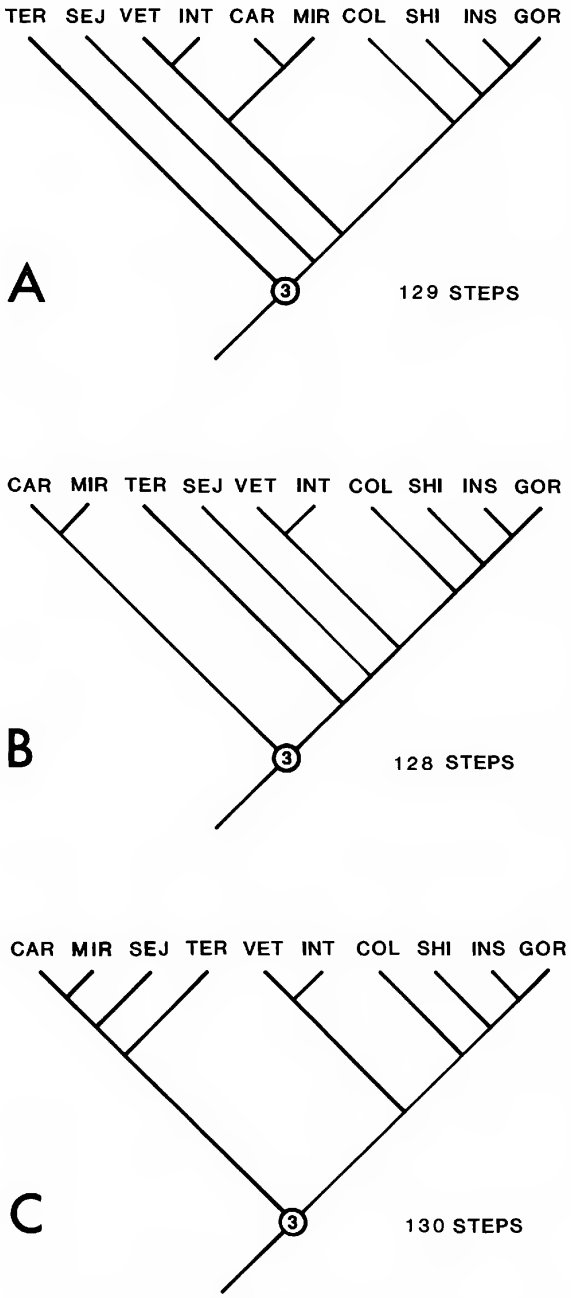

Fig. 11. Examples of slightly less parsimonious phylogenetic arrangements of merychippine equids than that shown in figure 10. In all 130 most parsimonious trees, Nodes 1–3 of figure 10 are the same, and differences are limited to the taxa above Node 3. Species abbreviations: TER, "*Merychippus*" *tertius*; SEJ, "*M.*" sp. near *sejunctus*; VET, *Protohippus vetus*; INT, "*M.*" *intermontanus*; CAR, "*M.*" *carrizoensis*; MIR, *Pliohippus mirabilis*; COL, "*M.*" *coloradense*; SHI, *Hipparion shirleyae*; INS, *M. insignis*; GOR, "*M.*" *goorisi*. **A.** ← "*M.*" sp. near *sejunctus* and "*M.*" *tertius* are displaced out of the Hipparionini and form successive sister groups to the Equini + Hipparionini. **B.** *P. vetus* and "*M.*" *intermontanus* are removed from the Equini and placed within the Hipparionini. **C.** As in B, but with "*M.*" *tertius* and "*M.*" sp. near *sejunctus* removed from the Hipparionini and placed in the Equini. The arrangement in B is equally parsimonious with that in figure 10 when characters are equally weighted, but is longer using scaled characters.

serves further testing with more taxa from each of the groups. However, the remainder of the study is based on the premise that equines and protohippines are each other's closest sister groups.

Even if the overall topology of the cladogram is assumed to be that of figure 10, there are numerous slightly less parsimonious variations one to three steps longer. For example, *Hipparion shirleyae* could be more closely related to "*M.*" *coloradense* than to *M. insignis* and "*M.*" *goorisi*; "*M.*" *tertius* and "*M.*" sp. near "*M.*" *sejunctus* could be united in a monophyletic group; *Protohippus vetus* could be more closely related to "*M.*" *carrizoensis* and *Pliohippus mirabilis* than to "*M.*" *intermontanus*; or "*M.*" *tertius* and "*M.*" sp. near "*M.*" *sejunctus* could be successive sister groups of the equines, protohippines, and hipparionines (fig. 11A). Again, further testing will determine which of the arrangements best fits the evolutinary history of the group. The following discussion presents the characters that support the arrangement of the taxa in figure 10.

The most parsimonious cladogram obtained in this study (fig. 10) is largely concordant with that found in a previous analysis (Hulbert, 1989). The differences are: (1) in the previous study, *Merychippus insignis* was considered the sister taxon of *Hipparion shirleyae* and "*M.*" *goorisi*; and (2) "*M.*" *isonesus* and "*M.*" *sejunctus* together formed a monophyletic group that was the sister taxon to all other hipparionines. In this study, the older "*M.*" *tertius* and "*M.*" sp. near "*M.*" *sejunctus* were used instead of "*M.*" *isonesus* and "*M.*" *sejunctus*, respectively, and in the most parsimonious arrangement, do not form a monophyletic group. Hulbert (1988a, 1989)

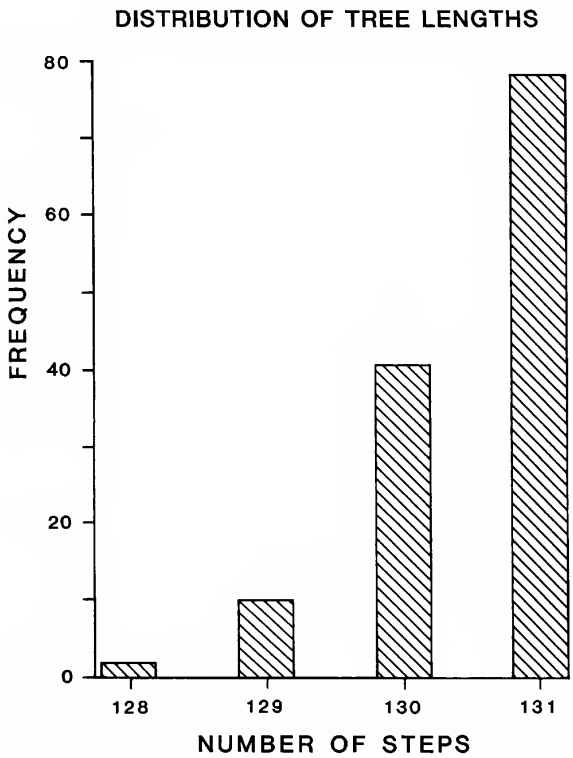

Fig. 12. Histogram of 130 shortest possible tree lengths for the 12 ingroup taxa based on the distribution of character states in table 1. They were obtained with the BBSAVE option of PAUP, using "*Parahippus*" *leonensis* as an outgroup, and equally weighted characters.

recognized two tribes of hypsodont horses, the Hipparionini and Equini, and both are monophyletic based on figure 10. The Hipparionini includes the taxa united at node 9, as well as their sister taxa *Neohipparion, Pseudhipparion, Merychippus* s.s., *Hipparion, Nannippus,* and *Cormohipparion* (plus some exclusively Old World clades) as is shown in figure 13 (Hulbert, 1988c, 1989). "*M.*" *tertius,* "*M.*" sp. near *sejunctus,* as well as "*M.*" *isonesus* and "*M.*" *sejunctus* s.s. were provisionally included in the Hipparionini by Hulbert (1988c, 1989). As this study suggests that protohippines could be more closely related to hipparionines than these taxa (fig. 11B), the provisional nature of this arrangement is emphasized. The sister group of the Hipparionini is the Equini, which includes the taxa united at node 4 in figure 10, as well as the genera *Calippus, Protohippus, Pliohippus, Astrohippus, Equus,* and *Onohippidium* (fig. 13; Hulbert, 1988a, 1989).

The core group of merychippine-grade hipparionines ("*M.*" *coloradense,* "*H.*" *shirleyae, M. insignis,* and "*M.*" *goorisi*) are united at node 9 of figure 10. Synapomorphies supporting this node are: more isolated protocones (27 and 28); well developed metastyle (35); a more persistent hypoconal groove on molars (39); and a hypoconal lake formed on premolars (40). The interrelationships of these four species and other hipparionines were studied in detail by Hulbert (1988c). "*Merychippus*" sp. cf. "*M.*" *sejunctus* shares with these four more persistent fossette plications (33), stronger protostylids (48 and 52), more persistently separated metaconids and metastylids (55), and increased unworn crown height (71). "*Merychippus*" *tertius* is the closest sister taxon of this group of five species (node 5, fig. 10) on the basis of only two putative synapomorphies: well-developed molar pli caballin (31); and greater articulation between the fourth and fifth metacarpals (79).

Equines and protohippines ("*M.*" *carrizoensis, P. mirabilis, P. vetus,* and "*M.*" *intermontanus*) are united at node 4 of figure 10, forming the sister group of the six hipparionines s.l., and represent the tribe Equini in this analysis. Node 4 is corroborated by six synapomorphies: a moderately deep DPOF (3) with a slight posterior pocket (5); ontogenetically rapid protocone connection on premolars (27); hypoconal lake on premolars (40); and unequal metaconid and metastylid size and position (67 and 68). "*Merychippus*" *carrizoensis* and *P. mirabilis,* two members of the subtribe Equina, share (node 7) a very deep DPOF (2) with a well-developed posterior pocket (5); a deep malar fossa (12); very rapidly connected protocones (27 and 28); weak premolar pli caballins (30); and simple internal fossette plications (33). These derived character states also unite them with more derived equines, such as *Equus, Pliohippus, Astrohippus, Onohippidium,* and *Hippidion* (fig. 13; Hulbert, 1989). The assessment of equine interrelationships shown in figure 13 is very provisional; this group is currently under study by BJM. "*Merychippus*" *intermontanus* and *P. vetus* share (node 6) wide preorbital bar (7); convex malar re-

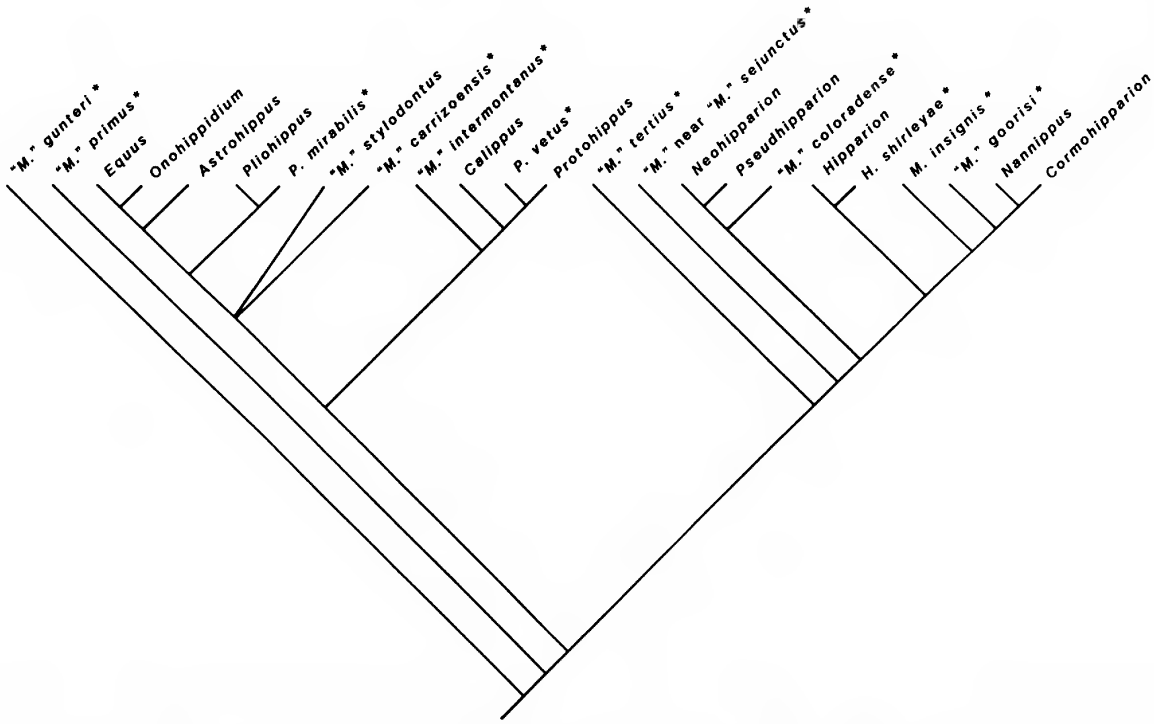

Fig. 13. Hypothesized phylogenetic relationships between the 12 merychippine taxa under study here (indicated by asterisks) and the 11 recognized hypsodont genera of North American Equinae. Topology based on the present study (fig. 10) with the 11 genera added following Hulbert (1987, 1988a, 1988c, 1989).

gion (11) (these two characteres are unknown for *P. vetus,* but are observed in the derived state in *P. perditus*); elongate-oval protocones (23); straighter upper cheekteeth (43); strong protostylids (48 and 52); and increased unworn crown height (71).

It has long been recognized that certain merychippines were closely related ("ancestral") to different genera of hipparionines and equines (Osborn, 1918: 98; Stirton, 1940: 180). Of the 12 taxa under study here, three are considered to be the primitive sister group of their respective genus: *Pliohippus mirabilis, Protohippus vetus,* and *Hipparion shirleyae* (fig. 13). The remaining nine are sister taxa to combinations of genera and therefore must be of generic rank or higher. Of the species studied, only *Merychippus insignis,* the type species of *Merychippus,* can be referred to that genus (although see Evander, 1986 and below), as it does not form a monophyletic group with any other merychippine species we have analyzed (fig. 13). Species not included in this study, e.g., *M. calamarius, M. californicus,* and *M. brevidontus,* might be referable to *Merychippus.* Six species ("*M.*" *carrizoensis,* "*M.*" *intermontanus,* "*M.*" *tertius,*"*M.*" sp. near *sejunctus,* "*M.*" *coloradense,* and "*M.*" *goorisi*) are here considered plesions of generic rank (Wiley, 1981), because they represent sister taxa of two or more valid, monophyletic genera. To include them in any genus shown in figure 13 would make it paraphyletic. Similarly, "*M.*" *primus,* "*M.*" *gunteri,* and "*Parahippus*" *leonensis* are considered to be plesions of tribal rank. The use of plesions is preferable at this time to the alternate of erecting nine new monotypic genera and three monotypic tribes.

TAXONOMIC STATUS OF *MERYCHIPPUS INSIGNIS* LEIDY, AGAIN

As previously noted, the type specimen of *Merychippus insignis* Leidy, 1874 is a frag-

mentary maxilla with a partial DP2 and a DP3 (ANSP 11276). Neither the stratigraphic context nor the exact geographic location where it was collected is definitely known. The inadequacies of the type were long recognized (e.g., Gidley, 1904; Quinn, 1955). More recently, two studies attempted to rectify this problem (Skinner and Taylor, 1967; Evander, 1986), but came to diametrically opposite conclusions. Skinner and Taylor (1967) first tried to better characterize the species with the addition of topotypic material. Several expeditions to the Bijou Hills by Skinner produced limited results, but did succeed in recovering a few permanent upper cheekteeth that can be referred to *M. insignis* with a reasonable degree of certainty. Second, using the dental characters observed on the type and topotypes, they sought a well-preserved quarry sample that matched these specimens in size and morphology. Skinner and Taylor (1967) suggested that cheekteeth from an extensive sample of skulls and maxillae from the early Barstovian Echo Quarry of western Nebraska were sufficiently close to be referred to *M. insignis.* Using the Echo Quarry and other samples, Skinner and Taylor (1967) and later workers (e.g., Voorhies, 1990) have characterized the cranial and permanent dental morphology of *M. insignis.* Evander (1986) argued against these methods on two grounds. First, he suggested that the methodology used by Skinner and Taylor is fundamentally flawed, because comparisons between the type material and possible matches is not definitive, too subjective, and too typological. Second, a more specific criticism, was that the Bijou Hills type of *M. insignis* and the referred Echo Quarry sample differed in what Evander interpreted as a species-level character, so that they could not belong to the same species. He concluded that the name *Merychippus* should only be applied to the topotypic material and a single specimen from the Texas Gulf Coastal Plain, and not to any recognizable generic clade of Miocene equids. We consider both of these arguments below, first the specific criticism, and then the general, based on a review of the same F:AM and TMM specimens studied by Evander.

Evander (1986) noted that the DP3 of ANSP 11276 lacked a distinct protostyle, which is a small cingular conule located between the protocone and paracone at the anterolabial corner of the tooth. He also noted that DP3s and DP4s from Echo Quarry all possess a protostyle. Skinner and Taylor (1967: 29) had previously concluded that protostyles were variably present in *M. insignis.* Evander's evidence that the presence or absence of a protostyle is a stable character in mesodont horses was based on observations of samples from Echo Quarry (all present) and Trinity River Pit 1 (all absent). He failed to discuss the polarity of this character. He also did not mention that similar cingular projections on lower cheekteeth (ectostylids, protostylids, and hypostylids) are notoriously variable in many populations of equids. The loss of these features occurred independently in many equid clades, and it is during the period of evolutionary loss when intraspecific variation is the greatest (e.g., the protostylids in *Nannippus lenticularis* and *N. aztecus*).

The large quarry samples of "*Parahippus*" *leonensis* and "*Merychippus*" *primus* from Thomas Farm and Thomson Quarry, respectively, were examined to determine the morphology of the protostyles on the DP3 and DP4. In both cases a continuum is observed ranging from a cingulum without a protostyle to presence of a very rudimentary conule to presence of a well-developed enamel growth several millimeters high (fig. 14). Moderate to well-developed protostyles were found on the majority of specimens (table 9), but the range of variation completely encompasses that observed on the type of *M. insignis* and in the Echo Quarry sample. The permanent upper cheekteeth of "*P.*" *leonensis* from Thomas Farm also have extremely variably expressed protostyles. Two deciduous premolars from Midway, Florida, that are referred to "*M.*" *gunteri* (UF/FGS V-4979 and V-9952) have relatively well-developed anterolabial cingula, but only weak protostyles. Another Midway specimen (UF/FGS V-9958) has a very weak labial cingulum, and no trace of a protostyle. Voorhies (1990) reported similar variation in the expression of the protostyle in the Norden Bridge sample of *Parahippus cognatus.* We conclude that, while in some populations a protostyle may be completely lacking and thus a stable character, in populations that have this feature

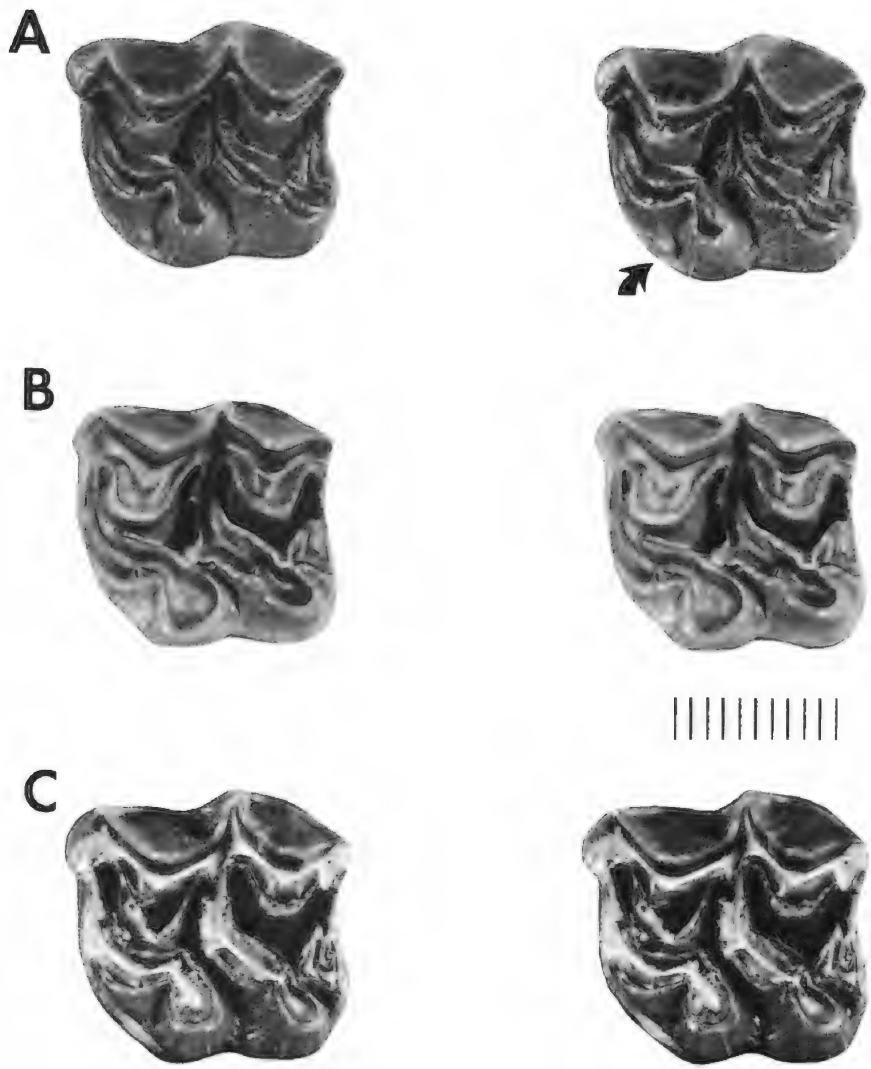

Fig. 14. Occlusal views of left upper deciduous premolars of "*Parahippus*" *leonensis* from Thomas Farm, Gilchrist County, Florida. These specimens display the different types of development of the protostyle observed in this population. **A.** UF 111, protostyle well developed. **B.** UF 99972, protostyle poorly developed. **C.** UF 99969, no protostyle present on anterolabial cingulum. Scale divided into millimeters.

its expression can be highly variable. The high degree of intraspecific variation for protostyle development makes it a poor indicator of phylogenetic relationships unless corroborated by other characters. The weak development of the protostyle on the type of *M. insignis* should not be the sole factor used to exclude the Echo Quarry sample from referral to that species.

Evander (1986) followed Quinn (1955) in referring a Texas Gulf Coastal Plain specimen to *Merychippus insignis* s.s. There is some confusion regarding exactly what specimen Quinn was discussing (Evander, 1986: 1277). Quinn (1955: 64) referred to a "complete deciduous dentition, B.E.G. [now TMM] no. 31242-84 . . . [that] includes the upper and lower first molars. . . ." As noted by Evander (1986), TMM 31242-84 does not include upper teeth or an m1 (rather it is an associated, moderately heavily worn right dp2-dp4 and left dp2). He assumed that Quinn referred

instead to TMM 31242-100, which consists of associated right and left maxillae with slightly worn DP2-DP4 and partially erupted, unworn M1s. There is a third pertinent specimen from this locality, TMM 31242-82, that consists of a right and a left unworn m1, and a left dp4. The latter tooth is clearly from the same individual as TMM 31242-84, and on it the last "2" in the catalog number has been changed to a "4". All of these specimens are very similar in their state of preservation, and the most reasonable supposition is that Quinn believed they all belonged to a single individual that he referred to by only one of its catalog numbers. This is not impossible, as there is no duplication of elements, but the degree of wear on the upper and lower deciduous premolars appears to be unequal. An association between the maxillae and the m1s of TMM 31242-82 is less unlikely, as the upper and lower molars are in the exact same stage of eruption. These specimens are important, because of the direct association of permanent and deciduous teeth. If, as determined by Quinn (1955) and Evander (1986), the deciduous premolars of TMM 31242-100 are the closest match to the type of *M. insignis,* then the morphology of the permanent teeth of *M. insignis* should also be like those of TMM 31242-100 and probably 31242-82. This would allow a check on the topotypes Skinner and Taylor (1967) referred to *M. insignis,* because that referral is uncertain without direct association of adult and juvenile teeth.

There are, however, several differing character states that tend to refute Quinn's referral of this material to *M. insignis.* Although both ANSP 11276 and TMM 31242-100 are slightly worn and thus do not have fully expressed fossettes, the degree of fossette complexity can be determined in each by looking into the cementless fossettes. In the type of *M. insignis,* all four fossette borders are plicated, with multiple plications for the pli prefossette and pli postfossette. The DP2 has a multiple pli protoloph. The fossette borders of TMM 31242-100 are much simpler, with shallower plications, and completely lack the pli protoloph or pli hypostyle; also the pli prefossette is single. The pli caballin is strong on ANSP 11276; weak or absent on TMM 31242-100. Finally, the latter is slightly larger and higher crowned at comparable wear stages. These differences appear to be systematically more important than the presence/absence of a protostyle. Overall, the morphology of the holotype resembles the samples of deciduous upper premolars from Echo Quarry and Lower Snake Creek much more than that of the Texas specimens.

TABLE 9

Protostyle Variation in "*Parahippus*" *leonensis*

[Distribution of the development of the protostyle on the DP3 and DP4 of the Thomas Farm population of "*P.*" *leonensis.* Three character states are recognized: (1) no protostyle developed on the anterolingual cingulum (fig. 14C); (2) small or rudimentary protostyle present (fig. 14B); and (3) protostyle large and well developed (fig. 14A). An asterisk (*) by the specimen number indicates a DP3, a plus (+) a DP4; all other specimens are isolated teeth that could be either DP3s or DP4s.]

No protostyle (N = 9)	Weak protostyle (N = 7)	Strong protostyle (N = 5)
UF 43613*	UF 99954*	UF 111
UF 43613+	UF 82	UF 58635
UF/FGS V-6452*	UF 162	UF 99963
UF/FGS V-6556A	UF 99970	UF 99967
UF 99964	UF 99972	UF 99973
UF 99965	UF 102700	
UF 99968	UF/FGS V-6556B	
UF 99969		
UF 99971		

Curiously, Evander (1986: 1278) noted that none of the recognized species from the Burkeville Fauna were ". . . large enough to represent adults of TMM 31242-100." However, TMM locality 31242 (part of the Point Blank Fauna of Hesse, 1943) is the type locality of *Protohippus vetus* Quinn (based on TMM 31242-71), a species whose molars match the size and simple morphology of the M1 of TMM 31242-100 (table 7). The m1 of TMM 31242-82 is not that of a hipparionine, as was stated by Quinn (1955), but instead closely resembles other Point Blank lowers referred to *P. vetus* in size and metastylid morphology (e.g., TMM 31242-103). We therefore follow Forstén (1975) in referring TMM 31242-100, -82, and -84 to the large protohippine in the Burkeville Fauna, *P. vetus,* and they should not be confused with *Merychippus.*

Evander's (1986) criticism of the method used by Skinner and Taylor (1967), finding a "best-match" for a poorly defined holotype, rests on two grounds. First, the method fails to account for variation. Evander (1986: 1278) hypothesized that: "It is possible that three or four species might encompass the morphology of a type specimen within their range of variation. The 'best-match' method forces an unjustifiable choice of one of these species." He ignored the fact that there is another, often used, option. If indeed the morphology of a type (plus topotypes if any) falls within the range of two or more truly distinct species, then a revisor has the recourse to declare the name a nomen dubium, and, if necessary in the best interests of nomenclatural stability, to submit an application to the International Commission on Zoological Nomenclature to officially suppress the name. Evander's second objection to the 'best-match' method is that it is subjective and nondefinitive. He postulated that after a type had been matched with a population (A), a new sample (B) might be discovered that differed from A, but which made a better match for the type. There are two solutions to this: (1) if the type falls within the range of variation for both A and B, then the situation is as described above; and (2) if the match with A can definitely be shown to be a mistake, the B can be referred to the species instead of A (which must then take a different name). Thus, the approach of Skinner and Taylor (1967) is valid. Their procedure involves the same steps as the referral of any population from outside the type area to a species, a judgment routinely made by all practicing systematists. What Evander's (1986) study does correctly bring out is that Skinner and Taylor (1967) only demonstrated that the type of *Merychippus insignis* matched the Echo Quarry sample, but did not show that it could not be referred to any other population. This would certainly be an arduous proposition in this particular case, given the large number of Barstovian merychippines. However, in cases like this where a name has been so widely used in the literature, such effort is justified rather than just expeditiously dismissing the name. Until such a study is completed, the Echo Quarry sample is retained as the reference point for *M. insignis*.

CHRONOLOGICAL AND BIOGEOGRAPHICAL DISTRIBUTION OF MERYCHIPPINES

Many staunch proponents of cladistic methodology advocate that chronological data have little or no value in phylogenetic analysis (e.g., Patterson, 1981). We believe that this view is extreme, particularly when the clade in question is chronologically well calibrated, as is the case for Miocene horses. Certainly only morphological data should be used to produce phylogenetic hypotheses for fossil taxa (Novacek and Norell, 1982). Then, available temporal data can be used to constrain the rate and timing of morphological transformation series, cladogenetic events, and changes in the geographic distribution of relevant taxa. When morphological data produce two or more equally parsimonious cladograms, biochronological distributions may suggest which of the hypotheses is more likely (Kemp, 1988a). In many cases, incongruence between morphological and temporal data suggest areas of future research. We assert that the most common causes of such discrepancies are "tardy" first-appearance datums, a not unexpected phenomenon considering the incompleteness of the sedimentary record. Other possible causes are misidentification or incorrect dating of specimens, or misinterpretation of poorly preserved material. Possible solutions in these cases include closer scrutiny of already collected specimens and efforts to collect new material; these may not entirely solve the problem, but rarely fail to provide some rewards.

In this section we review the temporal and paleobiogeographical ranges of the 13 species used in this study. Other taxa are also discussed when their distributions are relevant to the species under consideration here. For a chronological framework, we use the correlation of Neogene mammalian faunas presented by Tedford et al. (1988), along with the general time-scale calibrations of Berggren et al. (1985).

So far as is known, no hypsodont, or even incipiently hypsodont, equid taxa with cement-covered cheekteeth are known from any Arikareean or very early Hemingfordian deposits in North America. In the rich sequence of this period in, for example, Nebraska and

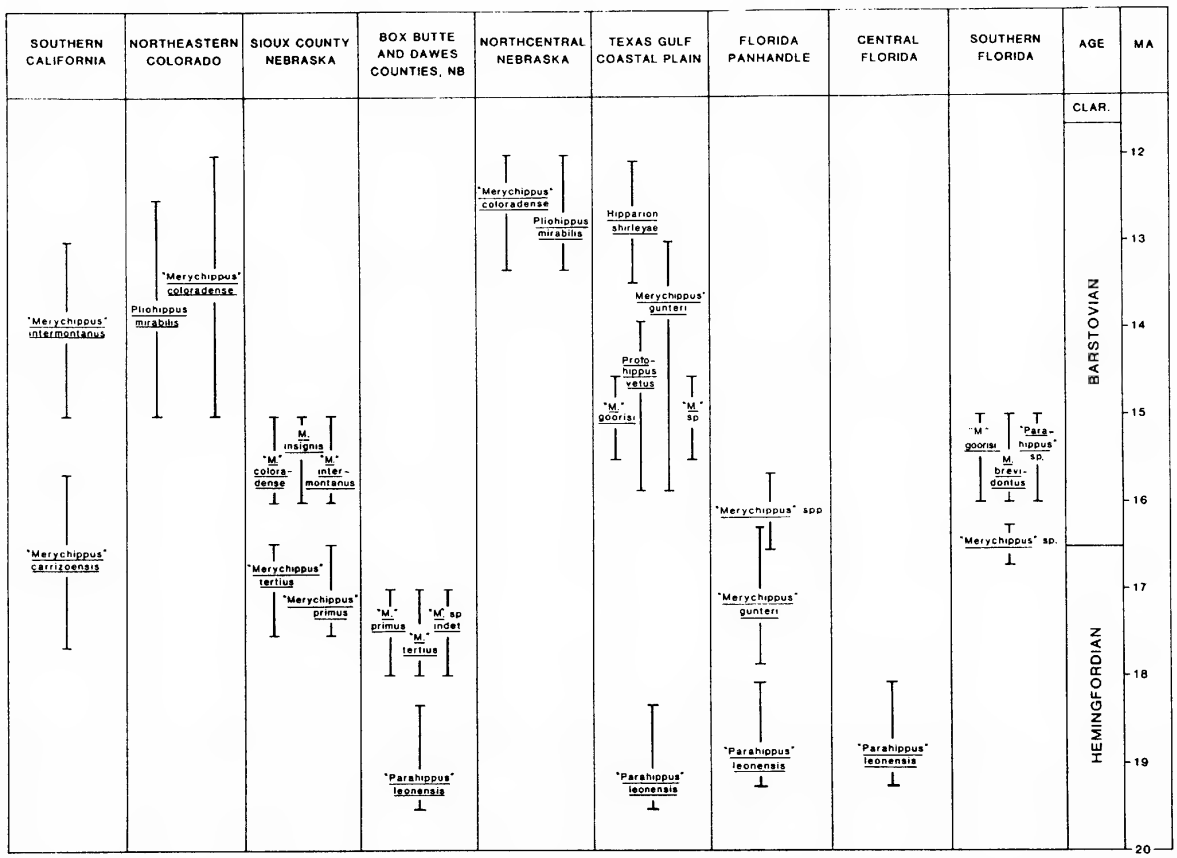

Fig. 15. Chronological and biogeographical distribution of the 13 taxa under study. Note that in many cases, especially in the Barstovian, there are additional species present in these faunas. The only taxa illustrated here which are not among the 13 species are new records from Florida being reported for the first time. Boundaries for land mammal ages and age of faunas after Tedford et al. (1988).

adjacent Wyoming, although there was a diversity of parahippines, all were brachyodont and lacked cement (Osborn, 1918; Schlaikjer, 1937).

As indicated above, the most likely sister group for all merychippines and more advanced equids is "*Parahippus*" *leonensis* (fig. 10). Although best known from localities in Florida, additional referred material is well known from Texas, and we present above a new description of a well-preserved specimen of this species from the Runningwater Formation of Nebraska. These localities are of late early Hemingfordian age, or about 19 to 18 Ma (fig. 15). This occurrence constrains the nearest common ancestor of all more advanced horses.

In what appears to be a very narrow time interval during the late Hemingfordian in Florida, ca. 17 to 18 Ma (Hunter and Huddlestun, 1982; Tedford and Hunter, 1984), there is only a single species of merychippine horse known, which is slightly more advanced than and possibly descended from "*P.*" *leonensis,* "*Merychippus*" *gunteri.* As mentioned above, there is a suggestion in the topotypic UF/FGS sample of this species that the population may actually consist of two morphologically similar ("sibling") species. Part of the sample (including the holotype) consists of broader and lower-crowned cheekteeth; others are narrower and higher-crowned. However, the small statistical sample is not sufficient to falsify a null hypothesis that only a single species is present. MacFadden and students (work in progress) are currently attempting to (1) collect additional specimens from the Torreya Formation; and

(2) calibrate the occurrence of "*M.*" *gunteri* and other merychippines in Florida using several geochronological methods. Although "*M.*" *gunteri* is also recognized from the Texas Gulf Coastal Plain, its occurrence there is Barstovian and therefore represents a range extension of this taxon relative to Florida (a nonfossiliferous zone in Texas [fig. 15] results in no late Hemingfordian localities, where "*M.*" *gunteri* might be expected to occur if present).

A similar pattern is apparent from the late Hemingfordian Red Division Fauna of the lower Barstow Formation in southern California, which is now radiometrically calibrated between 16.3 and 18 Ma (MacFadden et al., 1990; Woodburne et al., 1990). Only one species of "*Merychippus*" is present, the equine "*M.*" *carrizoensis*. At other late Hemingfordian sites in California, e.g., the Philips Ranch and Vedder l.f.s, "*M.*" *carrizoensis* is also the only apparent merychippine species present (Munthe, 1979; Quinn, 1987). However, in the Caliente Fauna (and also the Massacre Lake l.f. in Nevada), a second, larger species is known to co-occur with "*M.*" *carrizoensis* in the late Hemingfordian, but from very scanty material (Dougherty, 1940; Morea, 1981). Named "*M.*" *stevensi* by Dougherty (1940), this enigmatic form may in fact represent (1) "*M.*" *stylodontus,* (2) "*M.*" *tertius,* (3) the large, unnamed merychippine from the Box Butte Formation, or (4) a distinct taxon. Its ambiguous phylogenetic affinities notwithstanding, it demonstrates that a minimum of two merychippines were present in the late Hemingfordian of the West Coast. Woodburne et al. (1990) also reported an additional merychippine species from the latest Hemingfordian Rak Division Fauna in the Barstow Formation.

The earliest definite co-occurrence of three morphologically distinct species of "*Merychippus*" comes from the ca. 17.5–17.2 Ma Box Butte Formation of Nebraska (Galusha, 1975; he was very perceptive in his discussion of these horses, see p. 13 above and figs. 7G–I and 8H–J). The three species from this formation are represented by species referable to, or near, "*Merychippus*" *primus,* "*M.*" *tertius,* and a larger merychippine with hipparionine affinities. At least the first two of these taxa are well represented in the latest Hemingfordian Sheep Creek deposits of western Nebraska. These are the earliest records of the tribe Hipparionini, and are approximately coeval with the first occurrence of the Equini in California. Thus the age of the cladogenetic event that produced the tribes Equini and Hipparionini is constrained to a minimum of about 17.5 Ma.

The known Hemingfordian radiation of merychippine horses is summarized in figure 16. The initial phase started near the beginning of the late Hemingfordian (ca. 17.5–18 Ma). At least five distinct species resulting from a minimum of four cladogenetic speciation events were present in North America by the end of the Hemingfordian (figs. 15, 16). Present geochronological and biochronological resolution does not allow an exact temporal sequencing of the first occurrence of each individual taxon. The temporal interval represented by the unconformity between the Runningwater Formation (with no merychippines) and the overlying Box Butte Formation (three merychippines) is less than a million years (Tedford et al., 1988). During this interval (ca. 17.5 to 18 Ma), four of the cladogenetic speciation events shown in figure 16 must have occurred. This is the minimum age for the hypothetical common ancestor (Node 3 of fig. 10) of hipparionine and equine horses. Whether these events represent local speciation events in the Great Plains, or immigrations from other regions cannot be resolved without a much denser fossil record. It would seem that the power of geochronological resolution does not allow discernment of intracontinental dispersal of large, vagile mammals in the Tertiary, that must have durations of less than 10^5 years (Flynn et al., 1984) after the original speciation events.

During the early Barstovian, from about 16.5 to 15 Ma, a greater diversity of subhypsodont and hypsodont horses are represented at most sites across North America (figs. 15, 17). Branching patterns suggest that the absences of protohippines and "*Merychippus*" *stylodontus* from the late Hemingfordian (fig. 17) are artifacts of the fossil record (unless one or the other are represented by "*M.*" *stevensi*). Diversification had proceeded to a similar degree within each tribe, with at least five species from the Equini known by 15 Ma

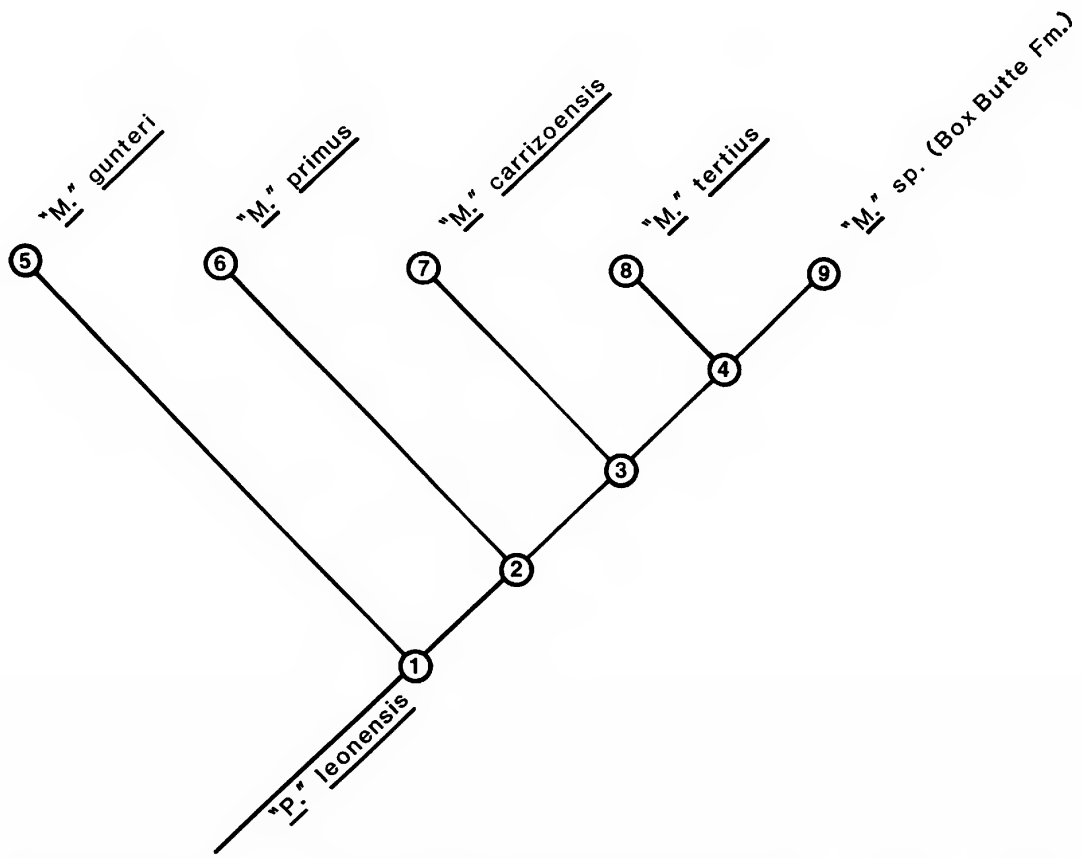

Fig. 16. Cladogram of the initial phase of the merychippine radiation. All merychippine taxa known to have existed by 17 Ma are shown. This cladogram is based on figure 10. Figure 16 hypothesizes that by 17 Ma, a minimum of five merychippine species had evolved from a common ancestor via four cladogenetic speciation events (Nodes 1–4). The distribution of character states among merychippines and their biostratigraphic ranges implies that two additional cladogenetic events (fig. 17) must have also occurred prior to 17 Ma, and that at least two additional merychippine species were present in the late Hemingfordian, but which are currently unrecognized in the fossil record (see text).

(two equines, three protohippines), and six hipparionine species.

The biogeographic distributions of these early Barstovian taxa show some provinciality. In Florida, the early Barstovian is still poorly known. Several sites from northern Florida stratigraphically higher in the Torreya Formation than the Midway l.f. have produced at least two equids more advanced than "*M.*" *gunteri* (which is also present), although larger samples and more complete material are needed before their alpha-level systematics can be elucidated (Bryant, 1988; fig. 9J, K). Somewhat better material from peninsular Florida (although primarily isolated teeth) derived from the Hawthorn Group (sensu Scott, 1988) indicates the presence of at least three merychippines. A small sample from the Arcadia Formation in Nichols Mine, Polk County is similar to "*M.*" *isonesus* or "*M.*" *sejunctus* (fig. 9A, B). Its age is regarded as early Barstovian on the basis of the stage of evolution of the heteromyid and cricetid rodents (A. E. Pratt and A. R. Poyer, personal commun.). A lower molar of a merychippine identical to those from Nichols Mine was recovered from the Hawthorn Group in extreme southwestern Hillsborough County (UF 53819). The slightly younger Sweetwater Branch Site from the Phosphoria Mine in Polk County produced two merychippines, "*M.*" *goorisi* and *M.* cf.

brevidontus (figs. 9C–I, 15). Altogether, a minimum of five merychippines are known form the early Barstovian of Florida: "*M.*" *gunteri,* "*M.*" *goorisi, M.* cf. *brevidontus,* "*M.*" cf. *isonesus* or *sejunctus,* and a small species close to "*M.*" *primus.*

The Burkeville Fauna of the Texas Gulf Coastal Plain includes five or six merychippines: the relictual "*M.*" *gunteri,* "*M.*" *goorisi,* "*Merychippus*" sp. cf. "*M.*" *sejunctus, Protohippus vetus,* a primitive *Calippus* sp. (Hulbert, 1988a), and possibly *M. insignis* (Skinner and Taylor, 1967). This record is derived from numerous local faunas (spanning about 2.5 m.y., Tedford et al., 1988), and they are not necessarily contemporaneous, as no single locality has produced all six. The Lower Snake Creek Fauna of Nebraska includes at least five merychippines: *M. insignis,* "*M.*" *isonesus,* "*M.*" *coloradense,* "*M.*" *intermontanus,* and a species near *P. vetus* (Skinner and Taylor, 1967; Skinner et al., 1977; MacFadden, 1984a). In contrast, the early Barstovian of the West Coast is much less diverse in terms of equids. The Mascall Fauna from Oregon (16–15 Ma, Tedford et al., 1988) has only three species, "*M.*" *isonesus,* the smaller "*M.*" *relictus,* and a low-crowned species like "*M.*" *brevidontus* (Downs, 1956; Woodburne, personal commun.). The Green Hills Fauna from the middle Barstow Formation, and strata of similar age from the Bopesta Formation of southern California usually contain only one or at most two merychippines, the more common "*M.*" *stylodontus,* and occasionally "*M.*" *carrizoensis* or *M. insignis* (Quinn, 1987; Woodburne et al., 1990).

By the early late Barstovian (13–14 Ma), more of the monophyletic generic clades appear in the fossil record. Joining *Merychippus, Protohippus,* and *Calippus* were *Pliohippus, Pseudhipparion, Cormohipparion, Hipparion,* and *Nannippus* (figs. 15, 17). *Neohipparion* should also be recorded from this time period, as it is the sister taxon of *Pseudhipparion* (Hulbert, 1987), but its first well documented appearance is early Clarendonian (*N. affine*). However, the Barstovian species "*M.*" *republicanus* was recently referred to *Neohipparion* by Voorhies et al. (1987) on the basis of unpublished material from western Nebraska. Description of these specimens could resolve the presently uncertain relationships between *Neohipparion, Pseudhipparion,* and "*M.*" *republicanus.* All other generic clades so far absent from pre-Clarendonian faunas are equines (*Astrohippus, Onohippidium,* and "*Dinohippus*"); they first definitely appear in the Hemphillian (Hulbert, 1989). The interrelationships among equines and the timing of their diversification are as yet poorly understood.

The middle Miocene radiation of the Equinae is summarized in figure 17. The interrelationships of the 13 equids studied here are based on figure 10; positions of other taxa are taken from Hulbert (1987, 1988a, 1988c, 1989). Figure 17 includes a conservative estimate of all species known to occur during a particular interval of time, and from all preceding intervals. By "conservative estimate" we mean that (1) very marginally represented taxa are excluded (e.g., "*M.*" *stevensi* or "*M.*" *relictus*), especially if they occur at only one locality and/or their position on a cladogram cannot be determined with much accuracy; and (2) pairs of species that are probably synonymous are regarded as a single taxon, even if the synonymy cannot be conclusively demonstrated with existing material. Figure 17 demonstrates in a general way the relative timing and pattern of diversification of the Equinae, and shows which clades first appear in the stratigraphic record later than is indicated by first appearance of their sister taxon ("tardy" first appearance datum). The alpha-level systematics of Barstovian equids is by no means completely understood. For example, the Frick Collection as organized by Morris Skinner contains several completely undescribed generic clades of merychippines. Thus, figure 17 should be interpreted only as a first approximation based on the current state of knowledge.

So far as we can discern the fossil record, the early phases of the radiation seemed to occur not in a localized area (contra Quinn, 1955), but were distributed throughout what is now the Gulf Coastal Plain and midcontinent. At this time, only localities in western North America, particularly southern California, suggest a separate biogeographic province and distinct endemism relative to eastern localities. Subsequent diversification of the principal clades during the Barstovian

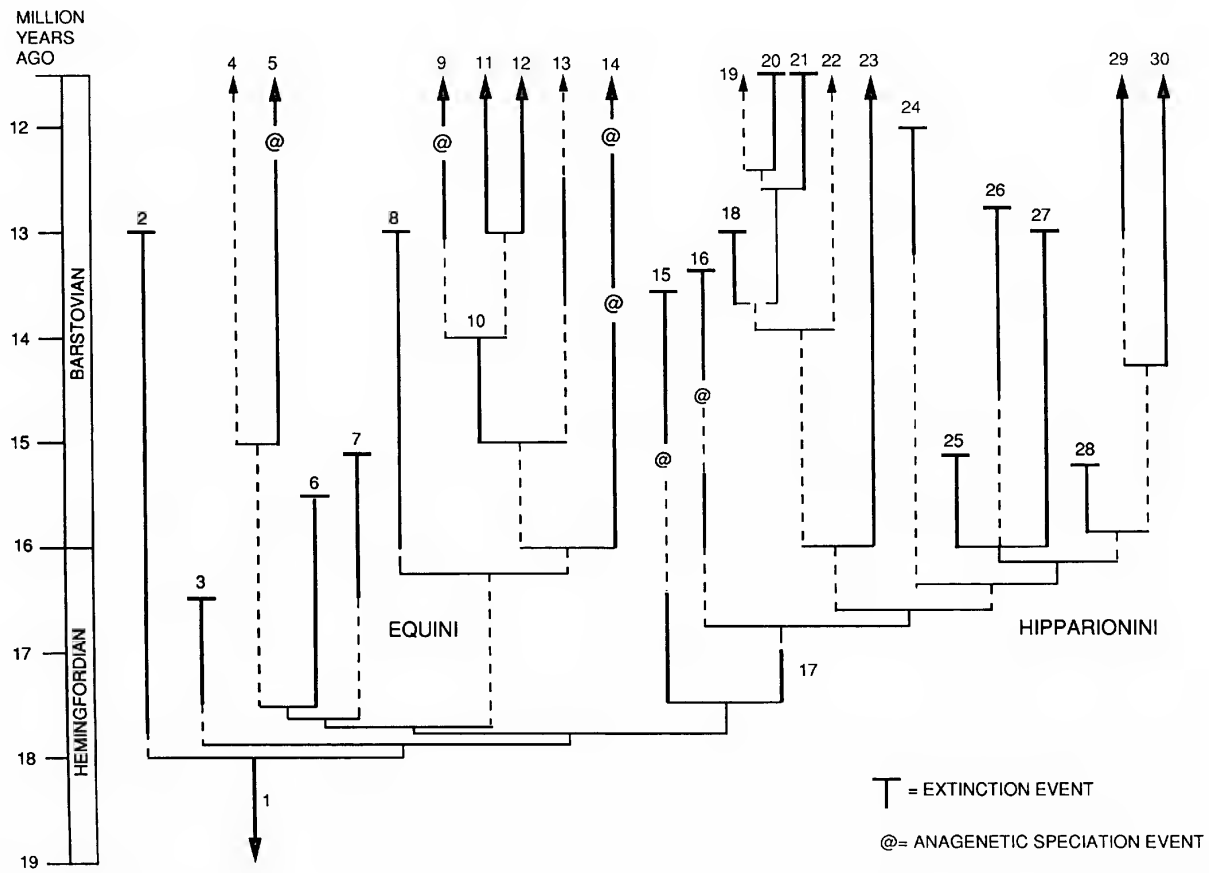

Fig. 17. Phylogenetic tree based on the results of cladistic analysis of North American equid species at the base of the adaptive radiation of hypsodont horses. The primary form of the tree is from figure 10, with additional data on younger taxa from Hulbert (1988a, 1988c, 1989). Temporal ranges of taxa based on authors' personal observations of specimens in the AMNH, TMM, UF, USNM, UCMP, and LACM collections. The numbered clades correspond to the following taxa: 1, "*Parahippus*" *leonensis*; 2, "*Merychippus*" *gunteri*; 3, "*M.*" *primus*; 4, *Astrohippus-Equus-Hippidion* clade; 5, *Pliohippus mirabilis-P. pernix*; 6, "*M.*" *carrizoensis*; 7, "*M.*" *stylodontus*; 8, "*M.*" *intermontanus*; 9, *Calippus proplacidus-C. placidus*; 10, *Calippus* sp. (Burkeville Fauna); 11, *Calippus* sp.-*Calippus elachistus* clade (Florida); 12, *C. regulus*; 13, *Calippus* (*Grammohippus*) clade; 14, *Protohippus vetus-P. perditus-P. supremus* clade; 15, "*M.*" *tertius*-"*M.*" *isonesus* clade; 16, "*Merychippus*" sp. cf. "*M.*" *sejunctus* (Trinity River l.f.)-"*M.*" *sejunctus* clade; 17, "*Merychippus*" sp. (largest species, Box Butte Formation); 18, "*M.*" *republicanus*; 19, *Pseudhipparion curtivallum-P. gratum* clade; 20, *Pseudhipparion* small sp. (Bradley Fauna, Florida); 21, *P. retrusum*; 22, *Neohipparion*; 23, "*M.*" *coloradense*; 24, "*Hipparion*" *shirleyae*; 25, *Merychippus insignis* (possible late Hemingfordian [Sheep Creek Fauna] and middle Barstovian [Norden Bridge l.f. and Pawnee Creek Fauna] populations not indicated); 26, *M. californicus*; 27, *M. brevidontus*; 28, "*M.*" *goorisi*; 29, *Nannippus*; 30, *Cormohipparion*. Slightly modified after MacFadden and Hulbert (1988, fig. 2).

was biogeographically complex. The equines remained most diverse in the West Coast and Great Basin, but a mid-Barstovian dispersal event resulted in their initial presence (by *Pliohippus mirabilis*) in the Great Plains and Gulf Coastal Plain. The majority of protohippines (*Calippus, Protohippus* s.s.) were limited to the Gulf Coastal Plain and Great Plains, and absent from western localities (Hulbert, 1988a). Only "*M.*" *intermontanus,* whose ties to the protohippines are somewhat equivocal, was present west of the Rocky

Mountains. As it is known from older faunas in the Great Plains than the West Coast, the direction of dispersal in this case was probably westward. Hipparionines were biogeographically heterogeneous. Many (e.g., "*M.*" *isonesus, Cormohipparion sphenodus, Neohipparion, Hipparion*) were widespread, although differing in areas of first appearance and dominance. Others (e.g., *Pseudhipparion,* "*M.*" *goorisi, Nannippus*) had more limited ranges, especially if examined at the subgeneric or species-group level. For example, *Cormohipparion* (*Notiocradohipparion*) is a small clade restricted to the Gulf Coastal Plain (predominantly Florida), but it persisted for about 9 m.y. (Hulbert, 1988b, 1988c).

CONCLUSIONS

For half a century, the hypothesized phylogeny of mid-Miocene Equinae as conceived by most authors has remained essentially unchanged (e.g., McGrew and Mead, 1938; Stirton, 1940; Simpson, 1951). Equinae originating from horizons stratigraphically equivalent to or higher than the Burge Formation were for the most part assigned to one of 11 hypsodont, "advanced" genera. Equids from underlying strata were assigned to the genus *Merychippus,* the putative ancestor of all of these younger genera. This artificially imposed boundary resulted in the interpretation that "generic" diversity of grazing equids increased dramatically about 12 Ma (e.g., Webb, 1983: fig. 2). Only a few instances of interrelatedness among the 11 hyposodont genera were indicated; in general they were each considered to have independently evolved from a separate merychippine ancestor (e.g., MacFadden, 1984a).

To test this phylogenetic scenario, we analyzed 12 relatively well-represented merychippine species using the PAUP computer software program. The exact phylogenetic relationships among these 12 merychippines remain to some extent poorly resolved. Reasons for the poor resolution include a high degree of homoplasy in the acquisition of certain character states, and inadequate representation in the fossil record of some of the taxa studied, so that many characters must be regarded as missing. While the analysis did produce a single, most parsimonious cladogram, there were numerous others of only slightly longer length (by 1 to 3 steps). Regardless of which cladogram truly reflects the evolutionary history of the group, all of those of minimal length imply the same general conclusions, at least for the initial phase of the radiation. The hypothesis that *Merychippus* as traditionally used is a monophyletic taxon is falsified, confirming the results of Evander (1989) and Hulbert (1989). Instead it is apparent that most merychippines either belong in one of the 11 recognized monophyletic clades of late Miocene horses (e.g., *Hipparion shirleyae, Protohippus vetus, Calippus proplacidus, Pliohippus mirabilis*), or represent sister taxa to monophyletic combinations of these 11 genera (e.g., the sister-group relationship of "*Merychippus*" *coloradense* to *Neohipparion* and *Pseudhipparion*). A very limited number of merychippine species form a monophyletic *Merychippus,* which necessarily includes the type species, *M. insignis.* The most parsimonious cladogram does not falsify a hypothesis that *Merychippus* is a member of the tribe Hipparionini, and that within this clade it is most closely related to "*M.*" *goorisi, Cormohipparion,* and *Nannippus* (see also Hulbert, 1988c).

"*Parahippus*" *leonensis* is considered to be the closest sister taxon of the merychippine radiation. During the early Hemingfordian (18–19 Ma), "*P.*" *leonensis* ranged from Florida to Nebraska, and, of its contemporaries, has the most synapomorphies with later merychippines. Merychippines first appeared almost simultaneously at about 17.5 Ma in Florida (Midway Fauna), Nebraska (Box Butte Fauna), northwestern Nevada (Massacre Lake l.f.), and southern California (Caliente, Philips Ranch, Vedder, and Red Division l.f.s). The scope, precision, and accuracy of present-day biochronological knowledge does not allow for a definitive sequencing of these first appearances. A minimum total of five merychippine species are represented in these faunas: "*M.*" *gunteri,* "*M.*" *primus,* "*M.*" *tertius,* "*M.*" *carrizoensis,* and an indeterminant, large merychippine with hipparionine affinities (Box Butte). An additional, poorly known, indeterminant species, "*M.*" *stevensi,* is known from California and possibly Nevada. Phylogenetic relationships of these and later taxa (figs. 13,

17) imply that two additional clades (one protohippine and one equine) must have also originated during this same interval, for a minimum total of seven late Hemingfordian merychippines. The transition from a single, widespread, advanced parahippine to seven geographically more restricted merychippines must have occurred very rapidly between 18 and 17 Ma. During this interval, however, the rate of morphological evolution was moderate relative to those calculated throughout the evolutionary history of the Equidae (MacFadden, 1988; MacFadden and Hulbert, 1988). Following this initial rapid burst of speciation in the late Hemingfordian, the rate of net growth in species numbers declined, but remained positive, until about 15 Ma.

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